PAPERS OF THE MICHIGAN ACADEMY OF SCIENCE ARTS AND LETTERS

VOLUME XLIII

(1957 Meeting)

PART I. NATURAL SCIENCE

NSP
RAW
MM
card

1958

COMMONWEALTH MYCOLOGICAL INSTITUTE
26 APR 1958

VOLUME XLIII CONSISTS OF THREE PARTS:

I. *Natural Science*

II. *Social Science*

III. *Philosophy, Literature, and Art*

Papers of the
MICHIGAN ACADEMY
OF SCIENCE, ARTS, AND LETTERS

VOLUME XLIII

(*1957 Meeting*)

Editor

SHERIDAN BAKER

PART I. NATURAL SCIENCE

ANN ARBOR · THE UNIVERSITY OF MICHIGAN PRESS

1958

COPYRIGHT © BY THE UNIVERSITY OF MICHIGAN 1958

LIBRARY OF CONGRESS CATALOG CARD NO.: 23–11028

PRINTED IN THE UNITED STATES OF AMERICA
WAVERLY PRESS • BALTIMORE • MD.

CONTENTS

Part I. Natural Science

GEOLOGY

Summary of North American Pleistocene Mammalian Local Faunas. Claude W. Hibbard 3
Occurrence of the Extinct Moose, *Cervalces*, in the Pleistocene of Michigan. Edmund A. Hibbard 33
The Dundee Limestone in Manistee County, Michigan. Lewis B. Kellum 39

MEDICINE

A Comparison of Acetylcholine and Potassium Citrate as Cardioplegic Agents. Carlos Mota, Thomas Gahagan, and Conrad R. Lam 53

ZOOLOGY

Some Ecological Observations of the Birds of Spring, Summer, and Fall on 64 Acres in Southern Michigan. H. Lewis Batts, Jr. 61
Benthic Associations of Sugarloaf Lake. Lee D. Beatty and Frank F. Hooper 89
A Preliminary Study of the Nutritional Ecology and Food Habits of the Chubs (*Leucichthys* Spp.) and Their Relation to the Ecology of Lake Michigan. Silvestre V. Bersamin ... 107
Notes of the Feeding Periodicity of Various Orthoptera. S. K. Gangwere 119
Notes on Nearctic Helcomyzidae and Dryomyzidae (Diptera Acalyptratae). George C. Steyskal 133

BOTANY AND FORESTRY

Studies in the Genus Fomes. I. Some Synonyms. Josiah L. Lowe. 147
Cruising Pole Timber by Bitterlich's Angle-Count Method. John Carow 151

PART I. NATURAL SCIENCE

GEOLOGY

Papers of the Michigan Academy of Science, Arts, and Letters
Vol. XLIII, 1958 (1957 Meeting)

SUMMARY OF NORTH AMERICAN PLEISTOCENE MAMMALIAN LOCAL FAUNAS

CLAUDE W. HIBBARD
University of Michigan

Introduction

The ages of various Pleistocene faunas have plagued geologists since the first recognition of glacial and interglacial intervals. The chief handicap in assigning Pleistocene faunas to different ages is the lack of faunas from the glaciated regions of North America which could provide controls for dating faunas from the nonglaciated regions. Faunas are unknown from tills, and only a few fossils are known from outwash gravel and sand or from interglacial deposits in the glaciated regions. With the exception of post-Sangamon deposits, no vertebrate fauna represented by more than a few specimens has been recovered from glaciated areas. Molluscan faunas, however, are known from Sangamon and Wisconsin deposits (Baker, 1920).

All the rich Pleistocene local faunas of North America have been recovered from areas outside of the glaciated region. There is, however, no direct stratigraphic correlation between most of the fossiliferous deposits in the nonglaciated region and the glacial deposits on which Pleistocene chronology is based. This does not mean that a direct correlation cannot be worked out. Such correlations will be made by the co-operative work of all specialists in Pleistocene geology.

The terms fauna and local fauna are often confused. The term fauna has many uses; "Pleistocene fauna," for example, includes all animal life of that time span. It can also be restricted to the Pleistocene fauna of a continent, country, or state. The term can be applied generally to the animal life of the different Pleistocene ages. It is unwise, however, to name a fauna after a time interval, since future work may change the age reference.

Local faunas, commonly named after a geographic locality, consist of an association of identifiable remains of animal life of the same age which have been collected in a restricted geographical area. Local faunal names should never be assigned to an isolated specimen. Only one of the Pleistocene local faunas is now well

enough known over a wide geographical area, and with sufficiently precise stratigraphic control, to be considered as a contemporaneous fauna. This is the Cudahy fauna which occurs in the base of the Pearlette ash and in the immediately underlying silt and silty clay. This fauna is known from Nebraska, Kansas, Oklahoma, and Texas.

Many local faunas, as well as isolated finds of vertebrate remains, have been reported from North America. Hay gives a compilation of these (1923, 1924, and 1927). Romer (1933) and Colbert (1937) have given good summaries of the Pleistocene fossil record in North America. A brief discussion of the problems encountered in age assignment of local faunas and use of provincial age and stage terms as applied to the Pleistocene follows. An explanation is given of the stratigraphic assignment of the local faunas in Table I.

Different Concepts of the Pleistocene

Zeuner (1950, p. 126) wrote, "the concept of Pleistocene time has developed along three almost independent lines." I list and briefly discuss these three different concepts here, since few students outside of the field of vertebrate paleontology are aware of these problems.

Typology—Lyell (1833) named certain units of Cenozoic rocks Older Pliocene and Newer Pliocene. He later (1839) applied the name Pliocene to what he previously called "Older Pliocene" and the name Pleistocene to the "Newer Pliocene." Calabrian and Villafranchian fossiliferous beds are present in the type section of Lyell's Pliocene. But these same beds, or their equivalents, occur in the base of Lyell's type section of his Pleistocene ("Newer Pliocene"). Some workers have considered the entire section at the type locality of Lyell's "Older Pliocene" as belonging in the Pliocene. Therefore, based on typology, the Pliocene has been considered by some workers to include the Calabrian and Villafranchian formations and their equivalents. The type localities of the Pliocene and Pleistocene are discussed by Gignoux (1913 and 1943), Movius (1949), and Stirton (1951). Vertebrate faunas from the Villafranchian deposits or equivalent deposits have been assigned to both Upper Pliocene and Lower Pleistocene by different workers who have failed to make clear that such age assignments were based upon Lyell's type sections.

At the 18th International Geological Congress in London in 1948,

the Pliocene-Pleistocene Boundary Commission recommended to the Congress that "in order to eliminate existing ambiguities, the Lower Pleistocene should include as its basal member in the type-area the Calabrian formation (marine) together with its terrestrial (continental) equivalent the Villafranchian." The Commission also noted "that according to evidence given this usage would place the boundary at the horizon of the first indication of climatic deterioration in the Italian Neogene succession" (see King, W. B. R., *et al.*, 1950, p. 6). This does not solve the problems in dating Pleistocene deposits and faunas throughout the world, but it does give a type section for the Pleistocene with which one may try to correlate.

Climatic criterion—Most students of earth science and vertebrate zoology in North America consider the terms Pleistocene, Ice Age, "Great Ice Age," or "Glacial epoch" as synonyms. In the teaching of historical geology the Pleistocene is distinguished from the rest of the Cenozoic by the evidence of glaciation. Flint (1947), Migliorini (1950), Osborn (1910), van der Vlerk (1950), and various textbooks of historical geology all consider that the above terms are synonymous and that the Pleistocene begins with the first climatic deterioration (marked cooling) at the end of the Pliocene.

Mammalian "index fossils"—As previously stated, the lack of vertebrate faunas from the earlier Pleistocene deposits of the glaciated regions of the Northern Hemisphere was a great handicap in interpreting the Pleistocene fossiliferous nonglacial deposits to the south. Osborn's *Age of Mammals* (1910) had an important influence on later work, both in Europe and North America. Osborn considered *Elephas columbi*(?), *Elephas imperator*, *Mastodon americanus*, *Equus complicatus* and *Equus occidentalis*(?), as characteristic of the first interglacial fauna. Although Osborn (1910, p. 373) considered the Pleistocene as synonymous with the Ice Age, his faunal lists were accepted in Europe and North America. He considered the Hay Springs fauna of Nebraska as Aftonian and the Blanco fauna of Texas as Pliocene. Those accepting Osborn's faunal list taught that the Pleistocene began with the first appearance of the modern horse, *Elephas*=*Mammuthus* and *Bison*. This was accepted in part by some European workers, whereas others contended that *Equus*, *Elephas*, and *Bos* occurred in the Upper Pliocene Villafranchian deposits. It was later recognized that both the genus *Plesippus* from the Blanco fauna of Texas and *Equus stenonis* from the Villa-

franchian faunas of Europe were zebrine horses (see Boule, 1900; McGrew, 1944).

Some workers consider the zebrine horses as generically distinct from the true horse, *Equus* (*sensu stricto*), and others consider the difference as only subgeneric. As recently as 1941, all faunas in North America that contained the zebrine horse *Plesippus* and the little three-toed horse *Nannippus* were assigned a late Pliocene age. None of the known faunas containing these two horses has been found to contain *Equus* (*sensu stricto*), *Mammuthus*, or *Bison* (see Wood, *et al.*, 1941). Though most of the vertebrate paleontologists in North America have taught that the Pleistocene is synonymous with the Ice Age, they have until recently considered all Pleistocene faunas that contained such fossils as *Stegomastodon*, *Plesippus*, and *Nannippus* as belonging in the Upper Pliocene. Thus the use of "index mammalian fossils" assigned some of the Pleistocene faunas to an earlier age.

The large mammals of the early Pleistocene faunas of North America are chiefly holdovers from the late Pliocene. In recent years it has been shown that some of the local faunas once considered as late Pliocene in age (such as the Coso Mountains, Blanco and Hagerman: Gazin, 1936; Hibbard, 1941; Wood, *et al.*, 1941), because of the presence of *Plesippus* and *Nannippus*, are actually early Pleistocene (Schultz, 1937; McGrew, 1944; Meade, 1945; Hibbard 1956a).

Colbert (1942, pp. 1510–1515), gives a good brief summary of previous methods of dating early Pleistocene mammalian faunas: "Those mammals particularly diagnostic of the beginning of the Pleistocene in North America are the modern horse, *Equus*, the mammoth, *Archidiskodon* [=*Mammuthus*], and cattle, *Bison*. To these three types there may be added the modern camelids, as exemplified in the New World by *Camelops*. Of the foregoing enumerated forms, the first and last were autochthonous and their first appearance marks the actual beginning of Pleistocene times in the North American region."

Today these statements need modification. *Equus* (*s. s.*) is unknown in North America before the late Kansan. The date of immigration of *Mammuthus* into North America is uncertain, but apparently is Aftonian or earlier. (A large collection of vertebrates from below the Pearlette ash in the Seymour formation of Texas

shows the mammoth had arrived there by late Kansan time. It could hardly have crossed the Bering Straits land bridge during a glacial age.) *Bison* is known only from later Pleistocene deposits.

Correlation with the type area—The establishment of a type area for the Pleistocene does not solve the problems of the Pliocene-Pleistocene boundary in North America. There are various means by which correlations of deposits and faunas with the type area may be attempted, such as fossil mammals, marine invertebrates, and the evidence of climatic change. The use of these three methods may not give the same results. The first evidence of a marked cooling of climate in North America seems to be the most reliable method to use for correlation with the type area in Italy, and hence for marking the beginning of the Pleistocene in North America. Evidence from Carbon-14 dating has shown that the later phases of the last glaciation were synchronous in Europe and North America, and it may be assumed that the other glaciations were also synchronous.

Correlation of Faunas

A control is needed to assign Pleistocene local faunas from the nonglaciated regions to given ages. Most of these faunas in North America come from widely scattered areas. Since an entire vertebrate fauna and the time and geographical ranges of its members cannot be completely known, it is difficult and even impossible at times to correlate local faunas that are chiefly known by different components. Stratigraphic controls do not exist in the nonglaciated regions since the Pleistocene deposits are not continuous.

Provincial Time Scales

Because of the lack of stratigraphic and faunal control on many of the fossil-bearing deposits in North America and the difficulty in correlating continental deposits with the European type sections, provincial stage and age names have been applied in North America. An example of such application is typified by the term Blancan.

Wood, *et al.* (1941) defined the Blancan age (Upper Pliocene) as the time range of *Borophagus*, *Ceratomeryx*, *Ischyrosmilus* and *Plesippus*, the last appearance of *Anancus* = *Stegomastodon*, *Lutravus*, *Megatylopus* = *Gigantocamelus*?, *Nannippus* and ?*Neohipparion*.

Borophagus, *Ceratomeryx*, *Ischyrosmilus*, *Plesippus*, *Nannippus*, *Stegomastodon*, *Lutravus* and *Gigantocamelus* are now also known from

early Pleistocene faunas such as the Blanco, Hagerman and Coso Mountains and have been shown to be of early Pleistocene age (Schultz, 1937; McGrew, 1944; Meade, 1945; Savage, 1955; Hibbard, 1956a). The Blancan provincial age of Wood, *et al.* (1941) by definition includes both late Pliocene and early Pleistocene faunas. At the present time the term Blancan is used for those faunas containing *Plesippus* and *Nannippus*, regardless of their Pliocene or Pleistocene age. The time-term Blancan should not be confused with the Blanco local fauna, which is one of the many faunas included in this provincial age.

Savage (1951, p. 289) defined the Irvingtonian provincial age as including those Pleistocene faunas that are post-Blancan in age and lack *Bison*. At this time he also named and defined the Rancholabrean provincial age, which includes the faunas that are post-Irvingtonian and are "denoted by their possession of the remains of *Bison* and by the presence of many mammalian species, particularly in the Carnivora and Rodentia, which are inseparable from Recent inhabitants of the same area."

Provincial age and stage names based on certain vertebrate associations found in different rock units are useful in dividing the Pleistocene into time and rock units in North America where direct stratigraphic correlations cannot be made with the glaciated section. In many parts of North America, in the nonglaciated areas, the Pleistocene deposits and their contained faunas either have not been studied in detail or are so poorly known that it is still impossible at the present time to assign the fossils to a given age of the Pleistocene.

Stratigraphic Control in Southwestern Kansas

I have attempted to work out a stratigraphic succession of Pleistocene local faunas for a local area in the nonglaciated region of North America and to correlate these faunas with the events recorded in the glaciated region. This area is in the Meade Basin in southwestern Kansas where more than 400 feet of Pleistocene deposits are known. In this area and in the adjoining part of northwestern Oklahoma the Pleistocene deposits are underlain by more than 500 feet of Pliocene deposits. This area of deposition is unusual in that the two older Pleistocene formations occur as

widespread sheet deposits on the underlying Pliocene. The two younger Pleistocene formations are not sheet deposits but abandoned valley fillings, terraces, or sinkhole deposits. A stratigraphic succession of local faunas has been recovered from these sediments. Some of the faunas consist of associated mollusks and lower vertebrates as well as mammals. This area provides a stratigraphic and faunal control for the Pleistocene local faunas by the underlying Upper Pliocene Rexroad formation and its contained local faunas, and by its recent fauna. This stratigraphic succession of Pleistocene faunas records, in part, the faunal movement, first appearance, and extinction of animal life with evidence of climatic changes in that region during the Pleistocene. These faunas can be tentatively correlated with the events in the glaciated region on the assumption that there were only four major continental glaciations and three major interglacial intervals in North America. On the basis of the correlation of these formations and their faunas in the Meade Basin with the events in the glaciated region, it is possible to extend a tentative age assignment to other known faunas, which in some cases lack a stratigraphic and faunal control in their local area.

Climatic Interpretation of Local Faunas

A local fauna must be carefully studied before assigning it to a glacial or an interglacial age. In the analysis of a fauna it is assumed, unless there is evidence to the contrary, that extinct animals had similar environmental requirements to those of their close living relatives. It is necessary to work with the entire fauna. In no case has it been found that the interpretations of the molluscan, fish, amphibian, reptilian or avian faunas associated with the mammalian fauna are antagonistic. They have been found to be complementary and have aided greatly the interpretation of past climatic and environmental conditions.

Some vertebrate collections cannot be considered as a unit fauna; they are assemblages consisting of both glacial and interglacial elements. One such is the well-known Cumberland Cave fauna of Maryland (Gidley and Gazin, 1938, pp. 10-63). The presence of a crocodile or an alligator with the remains of a boreal lemming, *Synaptomys* (*Mictomys*), indicates the mixture of an interglacial with a glacial fauna.

Pleistocene Local Faunas

I have reviewed all of the well-known Pleistocene faunas of North America. From this study I have attempted to compile a stratigraphic list of faunal occurrences using only those local faunas which I believe to have sufficient stratigraphic and faunal control to allow a tentative stage and age assignment prior to the Wisconsin.

I do not expect all workers to agree with the tentative age assignment of some faunas. Further study of the Pleistocene will provide much-needed information concerning the ages of North American Pleistocene faunas.

A great number of isolated finds of extinct mammals in North America occur in deposits of Wisconsin age, and especially in the drift area where their remains have been recovered chiefly from bog deposits. A number of these mammals have been lumped together under Wisconsin and have been assigned number 10, to indicate their occurrence in North America during Wisconsin time. For example, the remains of the American mastodon have been taken from hundreds of Wisconsin deposits in North America. It is impossible to list here all geographical occurrences of the American mastodon and those of other large mammals known chiefly from isolated finds.

The number preceding the faunal names is used in the tentative stratigraphic list of genera and species and to indicate bibliographic references to the faunas.

Wisconsin Local Faunas

1. Burnet Cave, New Mexico
2. Carpinteria, California
3. Cherokee Cave, Missouri
4. Craighead Caverns, Tennessee
5. Frankstown Cave, Pennsylvania
6. Gypsum Cave, Nevada
7. Hawver Cave, California
8. Jones Ranch, Kansas
9. McKittrick, California
10. North America
11. Papago Springs Cave, Arizona
12. Potter Creek Cave, California
13. Rampart Cave, Arizona
14. Rancho La Brea, California

15. Samwel Cave, California
16. San Josecito Cave, Mexico
17. Utah Cave, Utah
18. Ventana Cave, Arizona

Sangamon Local Faunas

19. Cragin Quarry, Kansas
20. Jinglebob, Kansas
21. Rezabek, Kansas

Illinoian Local Faunas

22. Berends, Oklahoma

Yarmouth Local Faunas

23. Borchers, Kansas

Kansan Local Faunas

24. Arkalon, Kansas
25. Cudahy (Fauna), Kansas, Nebraska, Oklahoma, Texas
26. Holloman, Oklahoma
27. Seger, Kansas

Aftonian Local Faunas

28. Blanco, Texas
29. Broadwater-Lisco, Nebraska
30. Coso Mountains, California
31. Deer Park, Kansas
32. Hagerman, Idaho
33. Sanders, Kansas

Transitional Nebraskan-Aftonian Local Faunas

34. Dixon, Kansas

Nebraskan Local Faunas

35. Unnamed assemblage from Angell member, Kansas
36. Sand Draw, Nebraska

Systematic List of Pleistocene Mammals

Table I lists the Pleistocene mammals of North America by orders and shows their stratigraphic occurrence in the more reliably dated

TABLE I

TENTATIVE STRATIGRAPHIC POSITION OF NORTH AMERICAN PLEISTOCENE MAMMALS

	Nebr.	Tr.	Aft.	Kan.	Yar.	Ill.	Sang.	Wisc.
Order Insectivora (Shrews and Moles)								
* *Sorex taylori* Hibbard—Taylor's shrew					23			
* *Sorex dixonensis* Hibbard—Dixon shrew		34						
* *Sorex leahyi* Hibbard—Leahy's shrew		34						
* *Sorex sandersi* Hibbard—Sanders' shrew			33					
* *Sorex cudahyensis* Hibbard—Cudahy shrew				25				
Sorex cinereus Kerr—Masked shrew				25		22	21, 20	8, 16
* *Sorex frankstounensis* Peterson—Peterson's shrew								5
Sorex cf. *trowbridgii* Baird—Trowbridge's shrew								2
Sorex saussurei Merriam—Saussure's shrew								16
Sorex cf. *ornatus* Merriam—Ornate shrew								2, 9, 14
* *Sorex* (*Neosorex*) *lacustris* (Hibbard)—Water shrew				25				
* *Microsorex pratensis* Hibbard—Plains pigmy shrew				25				
* *Blarina gidleyi* Gazin—Gidley's shorttail shrew			32					
* *Blarina fossilis* Hibbard—Fossil shorttail shrew							21	
Blarina brevicauda (Say)—Shorttail shrew						22	20	5
Cryptotis mexicana (Coues)—Mexican least shrew								16
Notiosorex crawfordi (Coues)—Desert shrew								14
Scapanus latimanus (Bachman)—California mole								12
Parascalops breweri (Bachman)—Hairytail mole								5
Order Primates (Man)								
Homo sapiens Linnaeus—Man								10
Order Chiroptera (Bats)								
Myotis cf. *velifer* (Allen)—Cave bat								11

Myotis cf. *evotis* (Allen)—Long-eared Myotis								11
Myotis cf. *thysanodes* Miller—Fringed Myotis								11
* *Corynorhinus tetralophodon* Handley—Big-eared bat								16
Corynorhinus cf. *rafinesquii* (Lesson)—Western big-eared bat								11
Antrozous pallidus (Le Conte)—Pallid bat								9, 11, 12
Tadarida cf. *mexicana* (Saussure)—Mexican freetail bat								11
Order Edentata (Sloths, Armadillos and Glyptodons)								
† *Nothrotherium shastense* Sinclair—Shasta ground sloth								6, 7, 12, 13, 14, 15, 18
† *Megalonyx leptostomus* Cope—Cope's ground sloth			28					
† *Megalonyx jeffersoni* (Desmarest)—Jefferson's ground sloth				26				9, 14
† *Paramylodon harlani* (Owen)—Harlan's ground sloth				26			20, 21	7, 9, 14
* *Dasypus bellus* (Simpson)—Beautiful armadillo								3
† *Glyptotherium texanum* Osborn—Texas glyptodon			28					
† *Xenoglyptodon fredericensis* Meade—Frederick glyptodon				26				
Order Rodentia (Squirrels, Rats and Mice)								
* *Aplodontia fossilis* Sinclair—Fossil aplodontia								12, 15
† *Paenemarmota barbouri* Hibbard & Schultz—Giant woodchuck			28, 29					
Marmota monax (Linnaeus)—Woodchuck								3
Marmota flaviventris (Audubon & Bachman)—Yellow-belly marmot								1, 11, 12, 13

Abbreviations: Nebr., Nebraskan; Tr., Transition between Nebraskan and Aftonian; Aft., Aftonian; Kan., Kansan; Yar., Yarmouth; Ill., Illinoian; Sang., Sangamon; Wisc., Wisconsin.

* Species extinct.

† Genus extinct.

TABLE I—*Continued*

	Nebr.	Tr.	Aft.	Kan.	Yar.	Ill.	Sang.	Wisc.
Order Rodentia (Squirrels, Rats and Mice) (*Cont.*)								
* *Cynomys meadensis* Hibbard—Meade prairie dog			31					
Cynomys ludovicianus (Ord)—Blacktail prairie dog								1, 8, 18
* *Citellus cragini* Hibbard—Cragin's ground squirrel					23			
* *Citellus meadensis* Hibbard—Meade ground squirrel					23			
Citellus richardsonii (Sabine)—Richardson's ground squirrel								8
Citellus variegatus (Erxleben)—Rock squirrel								1, 14
Citellus beecheyi (Richardson)—California ground squirrel								12, 15
Citellus lateralis (Say)—Golden-mantled squirrel								12, 15, 18
Eutamias sp.—Western chipmunk								2, 12
Sciurus griseus Ord—Western gray squirrel								15
Tamiasciurus douglasii (Bachman)—Chickaree								12, 15
Glaucomys sabrinus (Shaw)—Northern flying squirrel								12, 15
* *Thomomys gidleyi* Wilson—Gidley's pocket gopher			32					
* *Thomomys microdon* Sinclair—Sinclair's pocket gopher								12, 15
Thomomys bottae (Eydoux & Gervais)—Valley pocket gopher								1, 2, 9, 12, 14, 15
Thomomys talpoides (Richardson)—Northern pocket gopher								10
Thomomys umbrinus (Richardson)—Pigmy pocket gopher								1
* *Geomys tobinensis* (Hibbard)—Tobin pocket gopher			33	25				

* *Geomys quinni* McGrew—Quinn's pocket gopher	36		31					
Geomys sp.—Eastern pocket gopher					23	22	20, 21	8
Cratogeomys castanops (Baird)—Mexican pocket gopher								1
* *Perognathus pearlettensis* Hibbard—Pearlette pocket mouse			33		23			
Perognathus cf. *inornatus* Merriam—Mexican pocket mouse								9
* *Perognathus gidleyi* Hibbard—Gidley's pocket mouse					23			
Perognathus hispidus Baird—Hispid pocket mouse							21	
Perognathus californicus Merriam—California pocket mouse								14
† *Prodipodomys* sp.—Kangaroo rat			33					
Dipodomys nr. *ingens* (Merriam)—Giant kangaroo rat								9
Dipodomys ordii Woodhouse—Ord's kangaroo rat							20	1
Dipodomys agilis Gambel—Pacific kangaroo rat								14
† *Etadonomys tiheni* Hibbard—Tihen's pocket mouse					23			
Liomys sp.—Mexican pocket mouse								16
† *Paradipoides stovalli* Rinker & Hibbard—Stovall's beaver						22		
† *Procastoroides sweeti* Barbour & Schultz—Sweet's beaver	36		29, 31					
† *Castoroides ohioensis* Foster—Ohio giant beaver								10
† *Castoroides* sp.—Giant beaver				24		22	21	
* *Castor accessor?* Hay—Hay's beaver			32					
Castor canadensis Kuhl—Canada beaver								3, 15
* *Oryzomys fossilis* Hibbard—Fossil rice rat							20	
* *Sigmodon* cf. *intermedius* Hibbard—Intermediate cotton rat			33					

TABLE I—*Continued*

	Nebr.	Tr.	Aft.	Kan.	Yar.	Ill.	Sang.	Wisc.
Order Rodentia (Squirrels, Rats and Mice) (*Cont.*)								
* *Sigmodon hilli* Hibbard—Hill's cotton rat					23			
† *Cudahyomys moorei* Hibbard—Moore's mouse				25				
* *Reithrodontomys pratincola* Hibbard—Grassland harvest mouse					23			
Reithrodontomys cf. *montanus* (Baird)—Plains harvest mouse							20	
Reithrodontomys megalotis (Baird)—Western harvest mouse								14, 16
* *Peromyscus imperfectus* Dice—Dice's deer mouse								14
Peromyscus cf. *californicus* (Gambel)—California mouse								9
* *Peromyscus cragini* Hibbard—Cragin's white-footed mouse				25				
* *Peromyscus cochrani* Hibbard—Cochran's white-footed mouse							20	
Peromyscus maniculatus (Wagner)—Deer mouse								5, 15
Neotoma lepida Thomas—Desert woodrat								1, 9
Neotoma mexicana Baird—Mexican woodrat								1
Neotoma cinerea (Ord)—Bushytail woodrat								1, 12, 15
† *Bensonomys meadensis* Hibbard—Meade-Benson mouse			33					
* *Onychomys fossilis* Hibbard—Fossil grasshopper mouse					23			
* *Onychomys jinglebobensis* Hibbard—Jinglebob grasshopper mouse							20	
Onychomys leucogaster (Wied-Neuwied)—Northern grasshopper mouse								8
Onychomys torridus (Coues)—Southwestern grasshopper mouse								14

† *Mimomys* (*Cosomys*) *primus* (Wilson)—Wilson's vole			30, 32					
† *Pliophenacomys meadensis* (Hibbard)—Meade vole		34	33					
Phenacomys sp.—Boreal grassland vole				25				
Clethrionomys gapperi (Vigors)—Boreal redback vole								5
† *Pliopotamys meadensis* Hibbard—Meade amphibious vole	36	34	31					
† *Pliopotamys minor* (Wilson)—Idaho amphibious vole			32					
* *Ondatra kansasensis* Hibbard—Kansas muskrat				25				
Ondatra zibethicus (Linnaeus)—Muskrat							20, 21	
† *Pliolemmus antiquus* Hibbard—Ancient vole		34	31, 33					
* *Neofiber leonardi* Hibbard—Leonard's water rat							21	
* *Pedomys llanensis* (Hibbard)—Upland vole				25				
Pedomys ochrogaster (Wagner)—Prairie vole						22	20, 21	8
* *Pitymys meadensis* Hibbard—Meade shrub vole				25				
Microtus pennsylvanicus (Ord)– Meadow vole						22	20, 21	5, 8
Microtus californicus (Peale)—California vole								2, 9, 12, 14, 15
Microtus longicaudus (Merriam)—Longtail vole								1
Microtus mexicanus (Saussure)—Mexican vole								1
* *Microtus paroperarius* Hibbard—Tundra vole				25				
* *Synaptomys rinkeri* Hibbard—Rinker's bog lemming		34						
* *Synaptomys australis* Simpson—Simpson's bog lemming							20	
Synaptomys cooperi Baird—Southern bog lemming								5, 16
* *Synaptomys landesi* Hibbard—Landes' bog lemming					23			
Synaptomys borealis (Richardson)—Northern bog lemming				25				
* *Zapus sandersi* Hibbard—Sanders' jumping mouse			33					
* *Zapus burti* Hibbard—Burt's jumping mouse					23			
* *Zapus adamsi* Hibbard—Adams' jumping mouse							20	
Zapus hudsonius (Zimmermann)—Meadow jumping mouse								5
Erethizon dorsatum (Linnaeus)—Porcupine								3, 5, 15

TABLE I—*Continued*

	Nebr.	Tr.	Aft.	Kan.	Yar.	Ill.	Sang.	Wisc.
Order Carnivora (Wolves, Bears, Raccoons and Cats)								
* *Canis andersoni* Merriam—Anderson's coyote								14
* *Canis petrolei* Stock—Petrol coyote								14
* *Canis caneloensis* Skinner—Canelo coyote								11
Canis cf. *latrans* Say—Coyote	36							
Canis latrans Say—Coyote								1, 9, 14, 18
Canis lupus Linnaeus—Gray wolf								1, 9, 11, 14
† *Aenocyon dirus* (Leidy)—Terrible wolf								2, 5, 9, 12, 14, 18
† *Aenocyon milleri* Merriam—Miller's wolf								14
Vulpes fulva (Desmarest)—Red fox								1, 12
Vulpes macrotis Merriam—Large-eared kit fox								9, 18
Vulpes velox (Say)—Kit fox								1
Urocyon cinereoargenteus (Schreber)—Gray fox								2, 11, 14, 16
† *Borophagus diversidens* Cope—Cope's bone-eating dog			28					
† *Borophagus solus* (Stock)—Stock's bone-eating dog			30					
† *Arctodus haplodon* (Cope)—Cope's short-faced bear								5
† *Arctodus simus* (Cope)—Short-faced bear							20	9, 12, 14
* *Tremarctos mexicanus* Stock—Mexican spectacled bear								16
* *Ursus optimus* Schultz—Schultz's grizzly bear								9, 14
Ursus (*Euarctos*) *americanus* Pallas—Black bear								3, 5, 11, 15, 16
* *Bassariscus sonoitensis* Skinner—Sonoita ringtail cat								11
Bassariscus astutus (Lichtenstein)—Ringtail cat								1, 12, 13

Procyon lotor (Linnaeus)—Raccoon								3
† *Canimartes cumminsii* Cope—Cummins's mustelid			28					
† *Canimartes? idahoensis* Gazin—Extinct mustelid			32					
† *Canimartes? cookii* Gazin—Extinct mustelid			32					
† *Trigonictis kansasensis* Hibbard—Kansas grison	36							
Mustela frenata Lichtenstein—Longtail weasel								9, 12, 14, 15
Mustela nigripes (Audubon & Bachman)—Black-footed ferret								1
Taxidea taxus (Schreber)—Badger								1, 2, 8, 9, 11, 14, 18
Spilogale interrupta (Rafinesque)—Southern spotted skunk							20	
Spilogale gracilis Merriam—Southwestern spotted skunk								2, 9, 11, 14
Mephitis mephitis (Schreber)—Striped skunk								2, 5, 8, 9, 11, 12, 14, 15
Conepatus mesoleucus (Lichtenstein)—Hognose skunk								1
* *Lutra piscinaria* Leidy—Fish otter			29, 32					
* *Felis lacustris* Gazin—Lake cat			32					
* *Felis daggetti* Merriam—Daggett's cat								9, 14
* *Felis bituminosa* Merriam and Stock—Black cat								14
Felis concolor Linnaeus—Puma							19	1, 14
* *Panthera palaeoonca* Meade—Extinct jaguar			28					
* *Panthera atrox* (Leidy)—The fierce jaguar							19	9, 10, 14, 18
Panthera onca (Linnaeus)—Jaguar								4
Lynx rufus (Schreber)—Bobcat								1, 9, 12, 14
† *Smilodon californicus* Bovard—Sabre-tooth cat								9, 14
† *Smilodon* sp.—Sabre-tooth cat	36							

TABLE I—*Continued*

	Nebr.	Tr.	Aft.	Kan.	Yar.	Ill.	Sang.	Wisc.
Order Proboscidea (Mastodons and Mammoths)								
† *Stegomastodon mirificus* (Leidy)—Wonderful short-jawed mastodon	35, 36	.....	28, 31	27				
† *Stegomastodon priestleyi* (Hay & Cook)—Priestley's short-jawed mastodon	.....	.....	.....	26				
† *Rhynchotherium falconeri* Osborn—Falconer's mastodon	.....	.....	28					
† *Rhynchotherium* sp.—Mastodon	.....	.....	31					
† *Mammut cosoensis* (Schultz)—Coso mastodon	.....	.....	30					
† *Mammut americanus* (Kerr)—American mastodon	.....	.....	.....	.....	.....	.....	.....	5, 9, 10, 12, 14
† *Mammuthus haroldcooki* (Hay)—Cook's mammoth	.....	.....	.....	24, 26				
† *Mammuthus imperator* (Leidy)—Imperial mammoth	.....	.....	.....	.....	.....	.....	.....	2, 14
† *Mammuthus columbi* (Falconer)—Columbian mammoth	.....	.....	.....	.....	.....	.....	20	9, 14
† *Mammuthus jeffersoni* (Osborn)—Jefferson's mammoth	.....	.....	.....	.....	.....	.....	.....	10
† *Mammuthus primigenius* (Blumenbach)—Woolly mammoth	.....	.....	.....	.....	.....	.....	.....	10, 12
Order Lagomorpha (Rabbits and Hares)								
† *Hypolagus* sp.—Extinct rabbit	.....	.....	28, 31	.....	23			
† *Hypolagus furlongi* Gazin—Furlong's rabbit	.....	.....	32					
† *Hypolagus* cf. *vetus* Kellogg—The old rabbit	.....	.....	32					
† *Hypolagus limnetus* Gazin—Gazin's marsh rabbit	.....	.....	30, 32					
† *Alilepus? vagus* Gazin—Undetermined rabbit	.....	.....	32					
† *Nekrolagus* sp.—Dead rabbit	.....	.....	.....	.....	23			
Lepus townsendii Bachman—Townsend hare	.....	.....	.....	.....	.....	.....	.....	1
Lepus americanus Erxleben—Snowshoe hare	.....	.....	.....	.....	.....	.....	.....	5, 15

Lepus alleni Mearns—Antelope jackrabbit								1
Lepus cf. *californicus* Gray—Blacktail jackrabbit					23			
Lepus californicus Gray—Blacktail jackrabbit								9, 11, 14, 18
Sylvilagus floridanus (Allen)—Eastern cottontail								1, 5
Sylvilagus audubonii (Baird)—Desert cottontail								1, 9, 11, 12, 14, 15
* *Sylvilagus leonensis* Cushing—Leon cottontail								16
Sylvilagus bachmani (Waterhouse)—Brush rabbit								2, 9, 14
Order Artiodactyla (Peccaries, Camels, Deer, Pronghorns, Bison, Musk oxen, etc.)								
† *Mylohyus pennsylvanicus* (Leidy)—Pennsylvania peccary								5
† *Platygonus pearcei* Gazin—Pearce's peccary			32					
† *Platygonus bicalcaratus* Cope—Cope's peccary			28					
† *Platygonus alemanii* Duges—Aleman's peccary								11
† *Platygonus compressus* Le Conte—Le Conte's peccary								3, 8, 9, 12, 14
† *Platygonus* sp.—peccary	36		30, 31	26	23			
† *Gigantocamelus spatulus* (Cope)—Giant camel	36		28, 29	26				
† *Camelops kansanus* Leidy—Kansas camel							19	
† *Camelops hesternus* (Leidy)—Western camel								9, 14, 17
† *Camelops* sp.—camel	35, 36		28, 32					
† *Tanupolama blancoensis* Meade—Blanco long-legged llama			28					
† *Tanupolama hollomani* (Hay & Cook)—Holloman's long-legged llama				26				
† *Tanupolama stevensi* (Merriam & Stock)—Stevens's long-legged llama								9
Cervus sp.—Elk								11
† *Sangamona?* sp.—Extinct deer								1
Odocoileus virginianus (Zimmermann)—Whitetail deer								1, 5
† *Cervalces scotti* (Lydekker)—Scott's moose								5, 10
* *Rangifer? fricki* Schultz & Howard—Frick's caribou?								1

TABLE I—*Concluded*

	Nebr.	Tr.	Aft.	Kan.	Yar.	Ill.	Sang.	Wisc.
Order Artiodactyla (Peccaries, Camels, Deer, Pronghorns, Bison, Musk oxen, etc. (*Cont.*)								
Rangifer caribou (Gmelin)—Woodland caribou								10
Rangifer arcticus (Richardson)—Barren ground caribou								10
† *Capromeryx arizonensis* Skinner—Arizona four-horned pronghorn			29					9, 14
† *Breameryx minor* (Taylor)—Tar pit pronghorn							19	
† *Breameryx minimus* (Meade)—Least tar pit pronghorn			32					
† *Ceratomeryx prenticei* Gazin—Prentice's pronghorn								1, 11
† *Stockoceros onusrosagris* (Roosevelt & Burden)—Stock's pronghorn								16, 18
† *Stockoceros conklingi* (Stock)—Conkling's pronghorn								1, 9, 14
Antilocapra americana (Ord)—Pronghorn								10
* *Bos bunnelli* Frick—Bunnell's yak							20	
* *Bison latifrons* (Harlan)—Giant bison								10
* *Bison geisti* Skinner & Kaisen—Geist's bison								10
* *Bison crassicornis* Richardson—Richardson's bison								1, 9, 10, 14
* *Bison antiquus* Leidy—Ancient bison								10
* *Bison alaskensis* Skinner and Kaisen—Alaska bison								10
* *Bison preoccidentalis* Skinner and Kaisen—Early western bison								10
* *Bison occidentalis* Lucas—Western bison								10
* *Saiga ricei* Frick—Rice's gazelle—Antelope								13
* *Oreamnos harringtoni* Stock—Harrington's mountain goat								12
Oreamnos americanus (Blainville)—Mountain goat								10
† *Bootherium nivicolens* Hay—Snow muskox								10
† *Bootherium sargenti* Gidley—Sargent's muskox								

† *Symbos cavifrons* (Leidy)—Woodland muskox								10
† *Symbos tyrrelli* Osgood—Tyrrell's woodland muskox								10
* *Ovibos proximus* Bensley—Bensley's muskox								10
* *Ovibos yukonensis* Gidley—Yukon muskox								10
Ovibos moschatus (Zimmermann)—Muskox								10
† *Euceratherium collinum* Furlong & Sinclair—California shrub-ox								1, 7, 12, 15
† *Preptoceras sinclairi* Furlong—Sinclair's shrub-ox								1, 9, 15
Ovis canadensis Shaw—Bighorn sheep								1, 6
Ovis dalli Nelson—White sheep								10
Order Perissodactyla (Tapirs, Zebras, Asses, and Horses)								
* *Tapirus copei* Simpson—Cope's tapir				26				
Tapirus sp.—Tapir								14, 18
† *Nannippus phlegon* (Hay) Small three-toed horse	35		28, 31, 33	27				
† *Plesippus simplicidens* (Cope)—Plains zebra	35, 36		28, 31	27				
† *Plesippus shoshonensis* Gidley—Shoshone zebra			32					
† *Plesippus francescana* (Frick)—California zebra			30					
* *Asinus calobatus* (Troxell)—Stilt-legged ass				24				
* *Asinus conversidens* Owens—Mexican ass								1, 11, 16
* *Asinus littoralis* Hay—Mexican ass?				26				
* *Asinus francisci* Hay—Francis' ass							19	
* *Equus excelsus* Leidy—Plains horse								1
* *Equus scotti* Gidley—Scott's horse				24				
* *Equus pacificus* Leidy—Pacific horse				26				
* *Equus complicatus* Leidy—Eastern horse				26				
* *Equus niobrarensis* Hay—Niobrara horse							19	
* *Equus occidentalis* Leidy—Western horse								9, 12, 14, 15, 18
* *Equus lambei* Hay—Lambe's horse								10
* *Equus alaskae* Hay—Alaska horse								10

local faunas. Numbers refer to the list of faunas previously given, and to references.

In the compilation of the list no specimens were examined. The faunal lists were taken from the publications cited, but I have changed the names of living genera and species to accord with the *List of North American Recent Mammals* (Miller and Kellogg, 1955), except in the case of the bears where I followed Erdbrink's classification (1953). A few recent revisions of the larger extinct Pleistocene mammals (Simpson, 1941, 1945; Skinner and Kaisen, 1947) have also been followed. I have not recognized fossil subspecies.

I am indebted to Drs. Louis I. Briggs, William H. Burt, Donald F. Eschman, Richard F. Flint, Everett C. Olson, and Dwight W. Taylor, for reading the manuscript and offering valuable suggestions. The study was undertaken at the request of Richard F. Flint, who asked me to prepare a table showing the stratigraphic position of North American Pleistocene mammals for his book, *Glacial and Pleistocene Geology* (1957).

DISCUSSION

The following remarks concern the tentative age assignment of certain well-known faunas. Some other faunas not listed in the chart are discussed also.

Meade (1953) considers the Blanco fauna from Texas as Nebraskan. If the sediments were laid down in a lake during a glacial time, as Evans and Meade (1945) suggest, the environmental conditions would have been favorable for an abundant molluscan and small vertebrate fauna. This statement is based on study of the late Nebraskan Sand Draw local fauna of Nebraska and that of the transitional Nebraskan-Aftonian Dixon local fauna from south-central Kansas. Both assemblages indicate richer faunas and widespread moist conditions in this region at the close of Nebraskan time. A widespread cool, moist climate during late Kansan time is shown by the Cudahy fauna, reported from the Panhandle of Texas (Johnston and Savage, 1955) to South Dakota. I have listed the Blanco fauna as Aftonian since no molluscan fauna has been recovered from these well-exposed deposits.

The Holloman fauna (Meade, 1953) from near Frederick, Oklahoma, is not strictly a local fauna, but an assemblage of vertebrates of various ages. The older members of the Holloman fauna indicate

Kansan age. The basis for this age assignment is the topographic position of the deposit and the association of *Stegomastodon* and *Mammuthus*. The identification of the horses as given by Meade shows that the assemblage is post-earliest Kansan, that is, post-Blancan. The assemblage is pre-*Bison* in age and falls within the Irvingtonian provincial age. I have assigned a Kansan age to most of the mammals reported from this locality. There is some evidence of later channeling of the earlier sand and gravel (O. F. Evans, 1930).

The larger well-known faunas of whose age I am uncertain are listed and followed by citation and comments.

Aftonian? local fauna

Cita Canyon, Texas (Johnston and Savage, 1955; Savage, 1955).

Late Kansan and/or Yarmouth local faunas

Curtis Ranch, Arizona (Gazin, 1942).

Grand View, Idaho (Wilson, 1933).

Port Kennedy, Pennsylvania (Cope, 1899; Hibbard, 1955a); probably Yarmouth.

Rock Creek, Texas (Troxell, 1915).

Illinoian and/or Sangamon local faunas

Conard fissure, Arkansas (Brown, 1908; and Hay, 1924). Chiefly glacial and may include later elements; probably Illinoian.

Cumberland Cave, Maryland (Gidley and Gazin, 1938). Both glacial and interglacial elements.

Hay Springs, Nebraska (Matthew, 1918; Hay, 1924). This fauna has always been assigned to an earlier age. At present there is no evidence for an age earlier than Illinoian. The muskrat, *Ondatra nebrascensis* (Hollister), is larger and more advanced than *O. hiatidens* Cope from the Port Kennedy cave fauna and *O. kansasensis* Hibbard from the Cudahy fauna. *Microtus pennsylvanicus* (Ord) is a common element of the fauna (Hibbard, 1956b). This meadow vole is unknown from the earlier Cudahy fauna, but it appears as a common member in the Illinoian Berends fauna of Oklahoma and its equivalents in Kansas.

Kentucky assemblage, Kansas (Hibbard, 1952). Both glacial and interglacial elements. The rodents indicate Illinoian and Sangamon.

Slaton local fauna, Texas (Meade, 1952); probably Sangamon.

Don flora and fauna, Ontario, Canada (Coleman, 1894, 1901). This interglacial fauna is known chiefly from the mollusks. The vertebrate remains should be carefully restudied.

Students interested in the Pleistocene faunas of Florida are referred to the following papers: Gazin, 1950; Holmes and Simpson, 1931; Simpson, 1929.

Wisconsin local faunas

Space has prohibited listing all Wisconsin local faunas in the table. Many of these, such as the Fossil Lake (Oregon) local fauna, are in need of revision.

Students interested in the occurrence of Wisconsin man with Pleistocene vertebrates are referred to Sellards' *Early Man in America* (1952). Dr. Sellards lists at least 113 sites with bibliographic references. A number of these sites have been dated by Carbon-14. Jelinek (1957) discusses the stratigraphic occurrence of certain Wisconsin mammals in association with early man.

Faunal References

All numbers, both here and in Table I, refer to the list of local faunas.

Wisconsin Local Faunas

1. Schultz, C. B., and E. B. Howard. 1935. The Fauna of Burnet Cave, Guadalupe Mountains, New Mexico. Proc. Acad. Nat. Sci. Phila., 87: 273–298.
2. Wilson, R. W. 1933. Pleistocene Mammalian Fauna from the Carpinteria Asphalt. Carnegie Inst. Wash. Publ., No. 440: 59–76.
3. Simpson, G. G. 1949. A Fossil Deposit in a Cave in St. Louis. Amer. Mus. Nat. Hist. Novitates, No. 1408: 1–46.
4. Simpson, G. G. 1941. Discovery of Jaguar Bones and Footprints in a Cave in Tennessee. Am. Mus. Nat. Hist. Novitates, No. 1131: 1–12.
5. Peterson, O. A. 1926. The Fossils of the Frankstown Cave, Blair County, Pennsylvania. Ann. Carnegie Mus., 16 (2): 249–314.
6. Harrington, M. R. 1933. Gypsum Cave, Nevada. Southwest Mus. Papers, No. 8: 1–197.
7. Stock, C. 1925. Cenozoic Gravigrade Edentates of Western North America. Carnegie Inst. Wash. Publ., No. 331: 113.
8. Hibbard, C. W. 1949. Pleistocene Stratigraphy and Paleontology of Meade County, Kansas. Univ. Mich. Mus. Pal., Contrib., 7 (4): 86–87.
9. Schultz, J. R. 1938. A Late Quaternary Mammal Fauna from the Tar Seeps of McKittrick, California. Carnegie Inst. Wash. Publ., No. 487 (4): 111–215.

10. Frick, C. 1937. Horned Ruminants of North America. Amer. Mus. Nat. Hist., Bull., 69: 1–669.

Hay, O. P. 1923. The Pleistocene of North America and Its Vertebrated Animals from the States East of the Mississippi River and from the Canadian Provinces East of Longitude 95°. Carnegie Inst. Wash., Publ., No. 322: 1–499.

Hay, O. P. 1924. The Pleistocene of the Middle Region of North America and Its Vertebrated Animals. Carnegie Inst. Wash., Publ., No. 322A: 1–385.

Hay, O. P. 1927. The Pleistocene of the Western Region of North America and Its Vertebrated Animals. Carnegie Inst. Wash. Publ., No. 322B: 1–346.

Osborn, H. F. 1936. Proboscidea. Vol. 1, New York: Am. Mus. Press: 1–802.

Osborn, H. F. 1942. Proboscidea. Vol. 2, New York: Am. Mus. Press: 805–1675.

Sellards, E. H. 1952. Early Man in America. Univ. of Texas Press: 1–211.

Simpson, G. G. 1941. Large Pleistocene Felines of North America. Am. Mus. Nat. Hist. Novitates, No. 1136: 1–27.

Simpson, G. G. 1945. Notes on Pleistocene and Recent Tapirs. Am. Mus. Nat. Hist., Bull., 86 (2): 37–81.

Skinner, M. F., and O. C. Kaisen. 1947. The Fossil *Bison* of Alaska and Preliminary Revision of the Genus. Am. Mus. Nat. Hist., Bull., 89 (3): 123–256.

11. Skinner, M. F. 1942. The Fauna of Papago Springs Cave, Arizona, and a Study of *Stockoceros*. Amer. Mus. Nat. Hist., Bull., 80 (6): 143–220.

12. Merriam, J. C., and C. Stock. 1925. Relationships and Structures of the Short-faced Bear, *Arctotherium*, from the Pleistocene of California. Carnegie Inst. Wash., Publ. No. 347: 10.

13. Wilson, R. W. 1942. Preliminary Study of the Fauna of Rampart Cave, Arizona. Carnegie Inst. Wash., Publ., No. 530: 169–185.

14. Stock, C. 1949. Rancho La Brea—A Record of Pleistocene Life in California. Los Angeles Co. Mus., Sci. Ser. No. 13, Paleont. No. 8, 4th ed.: 3–81.

15. Stock, C. 1925. Cenozoic Gravigrade Edentates of Western North America. Carnegie Inst. Wash., Publ., No. 331: 113.

16. Cushing, J. E., Jr. 1945. Quaternary Rodents and Lagomorphs of San Josecito Cave, Nuevo León, Mexico. Journ. Mammal., 26 (2): 182–185.

Findley, J. S. 1953. Pleistocene Soricidae from San Josecito Cave, Nuevo León, Mexico. Univ. Kans. Mus. Nat. Hist. Publ., 5 (36): 633–639.

Handley, O., Jr. 1955. A New Pleistocene Bat *Corynorhinus* from Mexico. Journ. Wash. Acad. Sci., 45 (2): 48–49.

Stock, C. 1950. Bears from the Pleistocene Cave of San Josecito, Nuevo León, Mexico. Journ. Wash. Acad. Sci., 40 (10): 317–321.

17. Romer, A. S. 1929. A Fresh Skull of an Extinct American Camel. Journ. Geol., 37 (3): 261–267.

18. Haury, E. W. 1950. The Stratigraphy and Archaeology of Ventana Cave, Arizona. Albuquerque: University of New Mexico Press. 1–599.

Sangamon Local Faunas

19. Hibbard, C. W. 1949. Pleistocene Vertebrate Paleontology in North America. Geol. Soc. Am., Bull., 60: 1425.
20. Hibbard, C. W. 1955. The Jinglebob Interglacial (Sangamon?) Fauna from Kansas and Its Climatic Significance. Univ. Mich. Mus. Pal., Contrib., 12 (10): 179–228.
21. Hibbard, C. W. 1943. The Rezabek Fauna, a New Pleistocene Fauna from Lincoln County, Kansas. Univ. Kans. Sci., Bull., 29 Part 2, No. 2: 235–247.

Illinoian Local Fauna

22. Rinker, G. C., and C. W. Hibbard. 1952. A New Beaver, and Associated Vertebrates, from the Pleistocene of Oklahoma. Journ. Mammal., 33: 98–101.

Smith, C. L. 1954. Pleistocene Fishes of the Berends Fauna of Beaver County, Oklahoma. Copeia, No. 4: 282–289.

Taylor, D. W. 1954. A New Pleistocene Fauna and New Species of Fossil Snails from the High Plains. Occ. Pap. Mus. Zool., Univ. Mich., No. 557: 1–16.

Yarmouth Local Faunas

23. Hibbard, C. W. 1949. Pleistocene Stratigraphy and Paleontology of Meade County, Kansas. Univ. Mich. Mus. Pal., Contrib., 7 (4): 75–76.

Hibbard, C. W. 1954. A New *Synaptomys*, an Addition to the Borchers Interglacial (Yarmouth?) Fauna. Journ. Mammal., 35 (2): 249–252.

Kansan Local Faunas

24. Hibbard, C. W. 1953. *Equus* (*Asinus*) *calobatus* Troxell and Associated Vertebrates from the Pleistocene of Kansas. Kans. Acad. Sci., Trans., 56 (1): 111–126.
25. Hibbard, C. W. 1944. Stratigraphy and Vertebrate Paleontology of Pleistocene Deposits of Southwestern Kansas. Geol. Soc. Am., Bull., 55: 718–744.

Johnston, C. S., and D. E. Savage. 1955. A Survey of Various Late Cenozoic Vertebrate Faunas of the Panhandle of Texas—Part I: Introduction, Description of Localities, Preliminary Faunal Lists. Univ. Calif. Publ. Geol. Sci., 31 (2): 46–47.

Tihen, J. A. 1955. A New Pliocene Species of *Ambystoma*, with Remarks on Other Fossil Ambystomids. Univ. Mich. Mus. Pal., Contrib., 12 (11): 239–240.

26. Meade, G. E. 1953. An Early Pleistocene Vertebrate Fauna from Frederick, Oklahoma. Journ. Geol., 61 (5): 452–460.
27. Hibbard, C. W. 1951. Vertebrate Fossils from the Pleistocene Stump Arroyo Member, Meade County, Kansas. Univ. Mich. Mus. Pal., Contrib., 9 (7): 227–245.

Aftonian Local Faunas

28. Meade, G. E. 1945. The Blanco Fauna. Univ. Texas Publ., 4401: 509–556.
Savage, D. E. 1955. A Survey of Various Late Cenozoic Vertebrate Faunas of the Panhandle of Texas, Part II: *Proboscidea*. Univ. Calif. Publ., Bull. Dept. Geol., Sci., 31 (3): 51–74.

29. Barbour, E. H., and C. B. Schultz. 1937. An Early Pleistocene Fauna from Nebraska. Am. Mus. Novitates, No. 942: 1–10.
Barbour, E. H., and C. B. Schultz. 1939. A New Giant Camel. Univ. Neb. State Mus., Bull., 2 (2): 17–26.

30. Schultz, J. R. 1937. A Late Cenozoic Vertebrate Fauna from the Coso Mountains, Inyo County, California. Carnegie Inst. Wash., Publ., No. 487 (3): 77–109.

31. Hibbard, C. W. 1956. Vertebrate Fossils from the Meade Formation of Southwestern Kansas. Pap. Mich. Acad. Sci., Arts, and Letters, 41 (1955): 169–179.

32. Gazin, C. L. 1936. A Study of the Fossil Horse Remains from the Upper Pliocene of Idaho. Proc. U. S. Nat. Mus., 83, No. 2985: 281–320.
Gazin, C. L. 1938. Fossil Peccary Remains from the Upper Pliocene of Idaho. Journ. Wash. Acad. Sci., 28 (2): 41–49.
Wilson, R. W. 1933. A Rodent Fauna from Later Cenozoic Beds of Southwestern Idaho. Carnegie Inst. Wash., Publ., No. 440: 117–135.

33. Hibbard, C. W. 1956. Vertebrate Fossils from the Meade Formation of Southwestern Kansas. Pap. Mich. Acad. Sci., Arts, and Letters, 41 (1955): 179–196.

Transitional Fauna

34. Hibbard, C. W. 1956. Vertebrate Fossils from the Meade Formation of Southwestern Kansas. Pap. Mich. Acad. Sci., Arts, and Letters, 41: (1955): 160–169.

Nebraskan Local Faunas

35. Hibbard, C. W. 1956. Vertebrate Fossils from the Meade Formation of Southwestern Kansas. Papers Mich. Acad. Sci., Arts and Letters, 41 (1955): 156–160.

36. McGrew, P. O. 1944. An Early Pleistocene (Blancan) Fauna from Nebraska. Field Mus. Nat. Hist., Geol. Ser., 9 (2): 33–66.
Taylor, D. W. 1954. A New Pleistocene Fauna and New Species of Fossil Snails from the High Plains. Occ. Papers Mus. Zool. Univ. Mich., No. 557: 1–16.

LITERATURE CITED

Baker, F. C. 1920. The Life of the Pleistocene or Glacial Period. Urbana: University of Illinois Press. 1–476.

Boule, M. 1900. Observations sur quelques Equides Fossiles. Bull. Soc. Geol. France, Ser. 3, Vol. 27 (1899): 531–542.

Brown, Barnum. 1908. The Conard Fissure, a Pleistocene Bone Deposit in Northern Arkansas: With Description of Two New Genera and Twenty New Species of Mammals. Am. Mus. Nat. Hist., Mem., 9 (4): 157–208.

Colbert, Edwin H. 1937. The Pleistocene Mammals of North America and Their Relations to Eurasian Forms. *In* Early Man (G. G. MacCurdy, Ed.). New York: J. B. Lippincott Co. 173–184.

—— 1942. The Geologic Succession of the Proboscidea. *In* Proboscidea, Vol. II (by H. F. Osborn). New York, Am. Mus. Press, Chapter 22: 1510–1515.

Coleman, A. P. 1894. Interglacial Fossils from the Don Valley, Toronto. Am. Geol., 13: 85–95.

—— 1901. Glacial and Interglacial Beds Near Toronto. Journ. Geol., 9: 285–310.

Cope, E. D. 1899. Vertebrate Remains from the Port Kennedy Bone Deposit. Journ. Acad. Nat. Sci. Phila., 11: 193–267.

Erdbrink, D. P. 1953. A Review of Fossil and Recent Bears of the Old World, with Remarks on Their Phylogeny Based Upon Their Dentition. Drukkerij Jan de Lange-Deventer: 1–597.

Evans, G. L., and G. E. Meade. 1945. Quaternary of the Texas High Plains. Univ. Texas Publ. No. 4401: 485–507.

Evans, O. F. 1930. Probable History of the Holloman Gravel Pit at Frederick, Oklahoma. Okla. Acad. Sci., Proc., 10: 77–79.

Flint, R. F. 1947. Glacial Geology and the Pleistocene Epoch. New York: John Wiley and Sons. 1–589.

Gazin, C. L. 1936. A Study of the Fossil Horse Remains from the Upper Pliocene of Idaho. Proc. U. S. Nat. Mus. 83, No. 2985: 281–320.

—— 1942. The Late Cenozoic Vertebrate Faunas from the San Pedro Valley, Ariz. U. S. Nat. Mus., Proc., 92, No. 3155: 475–518.

—— 1950. Annotated List of Fossil Mammalia Associated with Human Remains at Melborne, Fla. Wash. Acad. Sci., Journ., 40 (12): 397–404.

Gidley, J. W., and C. L. Gazin. 1938. The Pleistocene Vertebrate Fauna from Cumberland Cave, Maryland. U. S. Nat. Mus., Bull., 171: 1–99.

Gignoux, M. 1913. Les Formations Marines Pliocènes et Quaternaires de l'Italie du Sud et de la Sicile. Annales Univ. Lyon, New ser., Vol. I (36): 1–693.

—— 1943. Géologie Stratigraphique. 3rd ed., Paris: 1–667.

Hay, O. P. 1923. The Pleistocene of North America and Its Vertebrated Animals from the States East of the Mississippi River and from the Canadian Provinces East of Longitude 95°. Carnegie Inst. Wash. Publ., No. 322: 1–499.

—— 1924. The Pleistocene of the Middle Region of North America and Its Vertebrated Animals. Carnegie Inst. Wash. Publ. No. 322A: 1–385.

—— 1927. The Pleistocene of the Western Region of North America and Its Vertebrated Animals. Carnegie Inst. Wash. Publ., No. 322B: 1–346.

Hibbard, C. W. 1941. Paleoecology and Correlation of the Rexroad Fauna from the Upper Pliocene of Southwestern Kansas, as Indicated by the Mammals. Kans. Univ. Sci. Bull., Vol. 27, Part 1, No. 6: 79–104.

—— 1952. Vertebrate Fossils from Late Cenozoic Deposits of Central Kansas. Univ. Kans. Contrib. Pal., Vertebrata, Art. 2: 1–14.

—— 1955a. Notes on the Microtine Rodents from the Port Kennedy Cave Deposit. Acad. Nat. Sci. Phila., Proc., 107: 87–97.

—— 1955b. The Jinglebob Interglacial (Sangamon?) Fauna from Kansas and Its Climatic Significance. Univ. Mich. Mus. Pal., Contrib., 12 (10): 179–228.

—— 1956a. Vertebrate Fossils from the Meade Formation of Southwestern Kansas Pap. Mich. Acad. Sci., Arts, and Letters, 41 (1955): 145–203.

—— 1956b. *Microtus pennsylvanicus* (Ord) from the Hay Springs Local Fauna of Nebraska. Journ. Pal., 30 (5): 1263–1266.

Holmes, W. W., and G. G. Simpson. 1931. Pleistocene Exploration and Fossil Edentates in Florida. Am. Mus. Nat. Hist., Bull., 59 (7): 383–418.

Jelinek, A. J. 1957. Pleistocene Faunas and Early Man. Pap. Mich. Acad. Sci., Arts, and Letters, 42 (1956): 225–237.

Johnston, C. S., and D. E. Savage. 1955. A Survey of Various Late Cenozoic Vertebrate Faunas of the Panhandle of Texas—Part I: Introduction, Description of Localities, Preliminary Faunal Lists. Univ. Calif. Publ. Geol. Sci., 31 (2): 27–50.

King, W. B. R., *et al.* 1950. Recommendations of Commission Appointed to Advise on the Definition of the Pliocene-Pleistocene Boundary. International Geol. Cong. Report, 18th Session, Great Britain, 1948, Part IX, Proc., Sec. H: 6.

Lyell, C. 1833. Principles of Geology. London, Vol. 3: 52–53.

—— 1839. On the Relative Ages of the Tertiary Deposits Commonly Called "Crag" in the Counties of Norfolk and Suffolk. Mag. Nat. Hist. (ed. Edward Charlesworth), 3 (31 n.s.): 323, footnote.

McGrew, P. O. 1944. An Early Pleistocene (Blancan) Fauna from Nebraska. Geol. Ser. Field Mus. Nat. Hist., 9 (2): 33–66.

Matthew, W. D. 1918. Contributions to the Snake Creek Fauna with Notes upon the Pleistocene of Western Nebraska. American Museum Expedition of 1916. Am. Mus. Nat. Hist., Bull., 38 (7): 183–229.

Meade, G. E. 1945. The Blanco Fauna. Univ. Texas Publ. No. 4401: 509–556.

—— 1952. The Water Rat in the Pleistocene of Texas. Journ. Mamm., 33 (1): 87–89.

—— 1953. An Early Pleistocene Vertebrate Fauna from Frederick, Oklahoma. Journ. Geol., 61 (5): 452–460.

Migliorini, C. E. 1950. Pliocene-Pleistocene Boundary in Italy. International Geol. Cong. Report, 18th Session, Great Britain, 1948, Part IX, Sec. H: 66–72.

Miller, G. S., Jr., and R. Kellogg. 1955. List of North American Recent Mammals. U. S. Nat. Mus., Bull., No. 205: 1–954.

Movius, H. L., Jr. 1949. Villafranchian Stratigraphy in Southern and Southwestern Europe. Journ. Geol., 57 (4): 380–412.

Osborn, H. F. 1910. The Age of Mammals in Europe, Asia and North America. New York: Macmillan Co. 1–635.

Romer, A. S. 1933. Pleistocene Vertebrates and Their Bearing on the Problem of Human Antiquity in North America. *In* The American Aborigines (D. Jenness, Ed.). Toronto: University of Toronto Press. 49–81.

Savage, D. E. 1951. Late Cenozoic Vertebrates of the San Francisco Bay Region. Univ. Calif. Publ., Bull. Dept. Geol. Sci., 28 (10): 215–314.

—— 1955. A Survey of Various Late Cenozoic Vertebrate Faunas of the Pan-

handle of Texas, Part II: *Proboscidea*. Univ. Calif. Publ., Bull. Dept. Geol. Sci., 31 (3): 51–74.

Schultz, J. R. 1937. A Late Cenozoic Vertebrate Fauna from the Coso Mountains, Inyo County, California. Carnegie Inst. Wash., Publ. No. 487: 75–109.

Sellards, E. H. 1952. Early Man in America. Austin: University of Texas Press. 1–211.

Simpson, G. G. 1929. Pleistocene Mammalian Fauna of the Seminole Field, Pinellas County, Florida. Am. Mus. Nat. Hist., Bull., 56 (8): 561–599.

—— 1941. Large Pleistocene Felines of North America. Am. Mus. Novitates, No. 1136: 1–27.

—— 1945. Notes on Pleistocene and Recent Tapirs. Am. Mus. Nat. Hist., Bull., 86 (2): 37–81.

Skinner, M. F., and O. C. Kaisen. 1947. The Fossil *Bison* of Alaska and Preliminary Revision of the Genus. Am. Mus. Nat. Hist., Bull., 89 (3): 123–256.

Stirton, R. A. 1951. Principles in Correlation and Their Application to Later Cenozoic Holarctic Continental Mammalian Faunas. International Geol. Cong., Report 18th Session, Great Britain, 1948, Part XI: 74–84.

Tihen, J. A. 1955. A New Pliocene Species of *Ambystoma*, with Remarks on Other Fossil Ambystomids. Univ. Mich. Mus. Pal., Contrib., 12 (11): 229–244.

Troxell, E. L. 1915. The Vertebrate Fossils of Rock Creek, Texas. Am. Journ. Sci., 39: 613–638.

van der Vlerk, I. M. 1950. Correlation between the Pliocene-Pleistocene Deposits in East Anglia and in the Netherlands. International Geol. Cong. Report, 18th Session, Great Britain, 1948, Part IX, Proc., Sec., H: 101–106.

Wilson, R. W. 1933. A Rodent Fauna from Later Cenozoic Beds of Southwestern Idaho. Carnegie Inst. Wash., Publ., No. 440: 117–135.

Wood, H. E. II, *et al.* 1941. Nomenclature and Correlation of the North American Continental Tertiary. Geol. Soc. Am., Bull., 52: 1–48.

Zeuner, F. E. 1950. The Lower Boundary of the Pleistocene. International Geol. Cong. Report, 18th Session, Great Britain, 1948, Part IX, Proc., Sec. H: 126–130.

Papers of the Michigan Academy of Science, Arts, and Letters
Vol. XLIII, 1958 (1957 Meeting)

OCCURRENCE OF THE EXTINCT MOOSE, *CERVALCES*, IN THE PLEISTOCENE OF MICHIGAN

EDMUND A. HIBBARD
University of Michigan

In October, 1953, E. W. and William Pudell, brothers, of Berrien Springs, Michigan, found a part of a *Cervalces scotti Lydekker* antler in marl, excavated on their land in the spring of 1951 while digging irrigation ponds. This find is in the SW¼ Sec. 21, T.6S., R.17W, Berrien County, southwestern Michigan. The fossil-bearing strata lay about 10 feet below the surface and is late Wisconsin (post-Cary) in age. Occurrence of this fossil antler was reported (in litt.) by Amos Green of Eau Claire, Michigan, and the specimen was donated to the University of Michigan Museum of Paleontology by the Pudells on May 10, 1956. I wish to thank Dr. C. W. Hibbard for permission to report on this record.

The *Cervalces* specimen (No. 33666, University of Michigan Museum of Paleontology) consists of the proximal portion of what is probably the left antler (Pl. I, Figs. 1 and 2). The specimen, measured along its dorsal curvature, is 650 mm. long and shows the typical *Cervalces* palmation and long beam. The greatest and least diameters at 50 mm. from the burr are 50.2 and 49.3 mm. At 100 mm. from the burr the diameters are 47.9 and 46.7 mm., respectively. The distance from the burr to the somewhat arbitrary point where palmation begins is approximately 185 mm. Perhaps the beam diameters listed below will best show the area of palmation.

Distance from dorsal surface of burr	Greatest beam diameter
170 mm.	49.4 mm.
180 mm.	52.8 mm.
190 mm.	54.5 mm.
200 mm.	60.1 mm.
210 mm.	73.0 mm.

Two recent papers on this genus point out that variations in beam length in the genus *Cervalces* probably are not of specific value. C. W. Hibbard (1940) thought that the difference in beam lengths be-

tween *C. scotti*, *C. roosevelti* Hay, and *C. borealis* Bensley may be attributable to size and age differences within the species *C. scotti*. Galbreath (1939) stated that differences in beam measurements between the several described species of *Cervalces* may indicate integrating populations between *C. scotti* and *C. alaskensis* Frick. He pointed out that the measurements showed an increase from east to west. His data show that this was true for all specimens known at that time, except *C. borealis* from Toronto. Additional data now available from Michigan and Kansas, however, do not fall into this size gradient. Perhaps the variations in size can indeed be wholly attributed to individual or age differences. Galbreath's data (*loc. cit.*), plus the available additional information, are given in the table below.

Species	Locality	Age	Beam Length
C. scotti	New Jersey, Mt. Hermon	Post-glacial	180 mm. (holotype)
C. scotti	Kansas, Topeka	Late Pleistocene	180 mm.
C. scotti	Michigan, Berrien Springs	Post-Cary	185 mm.
C. borealis	Ontario, Toronto	Probably Wisconsin	330 mm. (holotype)
C. roosevelti	Indiana, Hazelton	Probably post-glacial	268 mm.
C. roosevelti	Illinois, Ashmore I	Post-glacial	281 mm.
C. roosevelti	Illinois, Ashmore II	Post-glacial	260 mm.
C. roosevelti	Illinois, Beecher	Post-glacial	286 mm.
C. roosevelti	Illinois, Minooka	Post-glacial	204 mm.
C. roosevelti	Iowa, Denison	Wisconsin (*fide* Galbreath)	300 mm. (holotype)
C. roosevelti	Nebraska, Giltner	Kansan (*fide* Schultz)	330 mm.
C. alaskensis	Alaska, Fairbanks	Late Pleistocene-Frick	430 mm. (holotype)

R. L. Peterson (1952) lists *Alces alces* as the only species occurring in North America. This same species is also found in Europe. In contrast, four species of *Cervalces* have been described from North America. While a considerable amount of variation in size of antlers was noted above for this genus, it probably is no greater than that found in Recent forms of the moose. There appear to be few published data on beam lengths of moose antlers. Measurements of a series of specimens at the University of Michigan Museum of Zoology

MAP 1. Known fossil records of the Pleistocene moose, *Cervalces*

range between 65 and 125 mm., with an average of 77.5 mm. for 12 individuals. Only two beam measurements were greater than 90 mm. These were of young animals approximately two and a half years old whose antlers showed very little palmation. The one showing palmation at 125 mm. had a beam diameter measurement of 35 mm., which is considerably less than published beam diameter measurements for *Cervalces*.

The reported occurrences of *Cervalces* in North America are shown

in Map 1. It will be noted that, except for the Alaskan specimen, all records lie in a belt extending from the eastern edge of the great plains eastward to the Atlantic coast. All *Cervalces* finds have been referred to post-glacial or late Pleistocene age except the one from Nebraska (Cook, 1931), which was referred to the Kansan by Schultz *et al.* (1951). The genus is confined to North America. A somewhat similar genus, *Libralces*, also having the characteristic long antler beam, has been described from the late Pleistocene of Europe by Azzorali (1952). He stated that although their true phyletic relationship is not clear these two genera appear to be very closely related.

LITERATURE CITED

Azzorali, A. 1952. L'Alce di Seneze. Paleontogr. Ital., Pisa, 47: 133–141; pls. 15, 16.

Cook, H. J. 1931. A Pleistocene Fauna from Southern Nebraska. Journ. Mamm., 12: 273–280.

Frick, Childs. 1937. Horned Ruminants of North America. Bull. Amer. Mus. Nat. Hist., Vol. 59. 669 pp.

Galbreath, E. C. 1939. A Second Record of *Cervalces* from East Central Illinois. Journ. Mamm., 20: 507–508.

Hay, O. P. 1923. The Pleistocene of North America and Its Vertebrated Animals from the States East of the Mississippi River and from the Canadian Provinces East of Longitude 95°. Carnegie Inst. Wash., Publ. No. 322, 499 pp.

Hay, O. P. 1924. The Pleistocene of the Middle Region of North America and Its Vertebrated Animals. Carnegie Inst. Wash. Publ., No. 332A, 385 pp.

Hibbard, C. W. 1940. The Occurrence of *Cervalces scotti Lydekker* in Kansas. Trans. Kansas Acad. Sci., 43: 411–415, 2 pls.

Peterson, O. A. 1917. A Fossil-Bearing Alluvial Deposit in Saltville Valley, Virginia. Ann. Carnegie Mus., 11: 469–474.

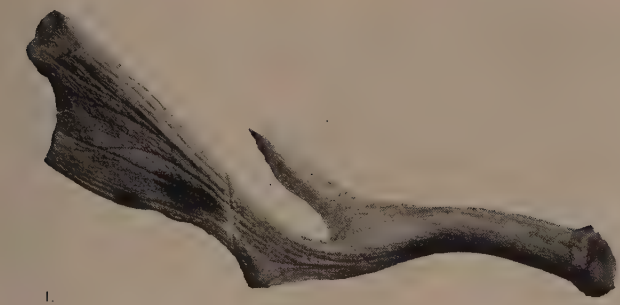
Peterson, O. A. 1926. The Fossils of the Frankstown Cave, Blair County, Pennsylvania. Ann. Carnegie Mus., 16: 249–315, 9 pls.

Peterson, R. L. 1952. A Review of the Living Representatives of the Genus *Alces*. Contrib. Royal Ontario Mus. Zool., No. 34: 28.

Riggs, E. S. 1936. Occurrence of the Extinct Moose, *Cervalces*, in Indiana and in Illinois. Amer. Midl. Nat., 17: 664.

Riggs, E. S. 1938. A Pleistocene Bog Deposit and Its Fossil Fauna. Trans. Ill. Acad. Sci., 29: 186–189.

Schultz, C. B., *et al.* 1951. A Graphic Résumé of the Pleistocene of Nebraska (with notes on the fossil mammalian remains). Bull. Univ. Nebr. State Museum, 3 (6): 1–41.



1.

2.

FIG. 1. Part of left antler, *Cervalces scotti*, UMMP No. 33666, Berrien County, Michigan, posterior view, × 4

FIG. 2. Part of left antler, *Cervalces scotti*, UMMP No. 33666, Berrien County, Michigan, dorsal view, × 3

Papers of the Michigan Academy of Science, Arts, and Letters
Vol. XLIII, 1958 (1957 Meeting)

THE DUNDEE LIMESTONE IN MANISTEE COUNTY, MICHIGAN

LEWIS B. KELLUM
University of Michigan

Introduction

The Dundee limestone is the most important oil-producing formation in Michigan. It does not crop out in Manistee County, but has been penetrated by some 35 wells in search of oil, salt, or brine. Shows of oil or gas have been recorded in the Dundee limestone in some of these wells, but no commercial production has been developed to date.

Manistee County is on the western side of the Lower Peninsula (Fig. 1). It is bounded on the west by Lake Michigan, on the south by Mason and Lake counties, on the east by Wexford County, and on the north by Benzie County.

The writer had the opportunity to study the Dundee limestone in five brine wells in southwestern Manistee County. It seemed worthwhile to record the information and to try to fit it into the larger picture of the formation in the county and in the state.

Wells from adjacent parts of the bordering counties have been used to supplement the information obtained from wells drilled in Manistee County.

No attempt has been made to differentiate between the Rogers City limestone and Dundee limestone. They are considered together in this investigation and are here referred to as the Dundee limestone.

Lithologic Character

The wells examined are in Manistee and Stronach townships. They are numbered 1, 2, 9, 10, and 11 on the maps. In well No. 1 the Dundee is medium and light gray limestone 80 feet thick. It contains some fine-grained sandstone and some gypsum. In well No. 2 it is 145 feet thick. The upper 30 feet is brown crystalline limestone; the lower 115 feet is brown crystalline dolomite and medium gray dolomite. The contact with the overlying Bell shale is

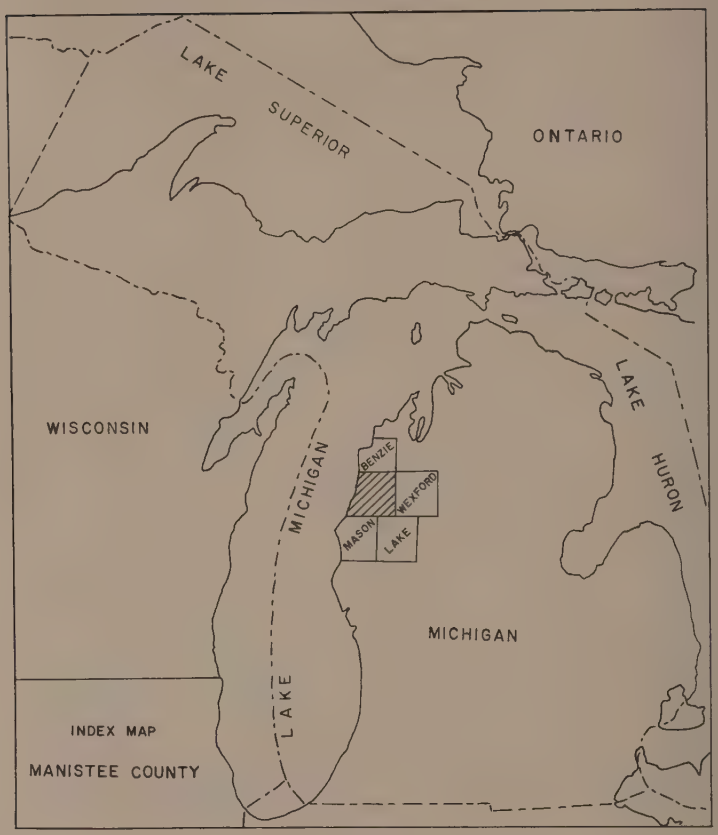
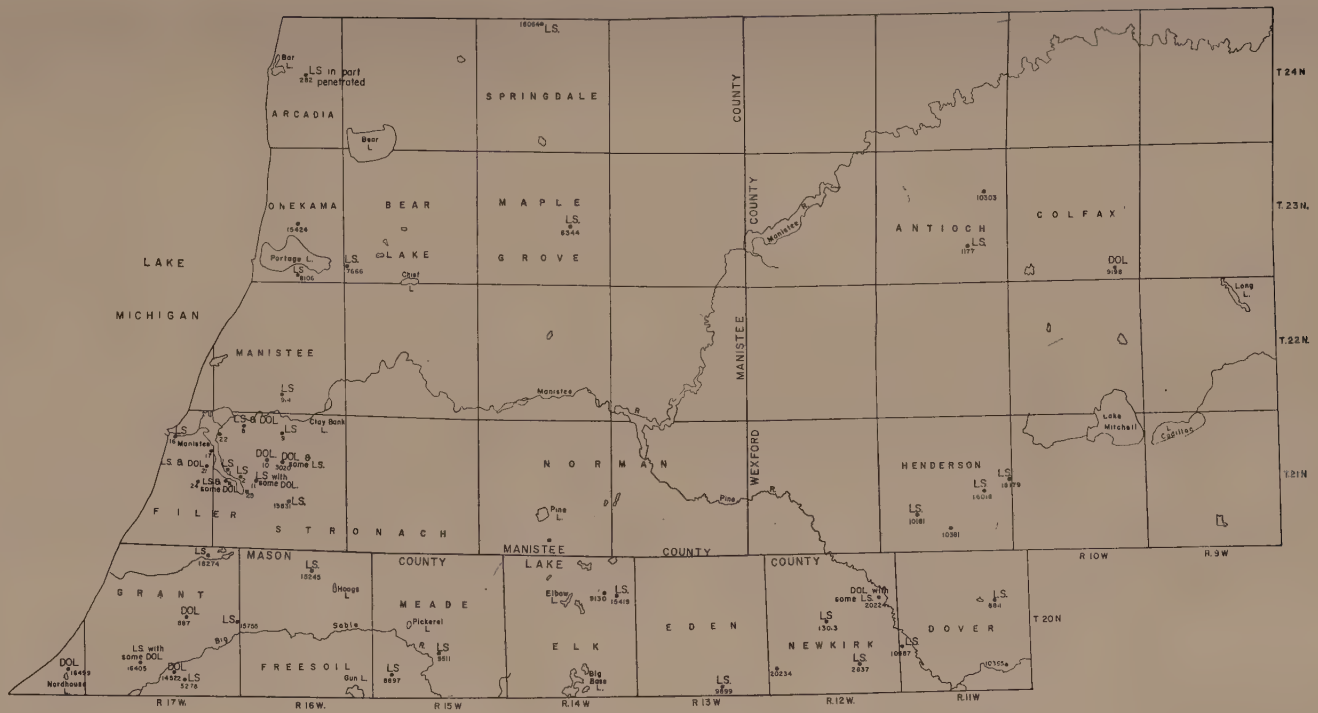


Fig. 1

sharp and easily recognized. The contact with the underlying Detroit River Group was located at the first conspicuous anhydrite in the sample. In Well No. 9 the Dundee is brown, finely crystalline limestone impregnated with bituminous material. In Well No. 10 it is predominantly brown crystalline dolomite with some limestone and anhydrite.

In Well No. 11 the Dundee consists of interbedded brown and gray dolomitic crystalline limestone. Under the microscope the

DUNDEE LIMESTONE, MANISTEE COUNTY, MICHIGAN



PRINCIPAL ROCK TYPES OF DUNDEE ENCOUNTERED IN WELLS

FIG. 2

brown limestone is seen to have many tiny openings which give it porosity. The brown color is due largely to the presence of oil in this porous limestone. In Wells No. 2 and No. 11 the formation is very similar but in Well No. 10 it is brown crystalline dolomite. The contact between the Dundee and the Detroit River formation in Well No. 11 is drawn where the rock changes from light brown, granular, finely crystalline limestone above, to medium gray, dense dolomite below. The dolomite appears in the sample from 1915–1920, which is predominantly limestone. In Well No. 10 the contact is similar in appearance but the Dundee above is dolomite instead of limestone. The similarity in appearance of the Dundee limestone in Well No. 11 and the Dundee dolomite in Well No. 10 is striking. Both are light brown, granular, and finely crystalline rock, but in Well No. 11 the Dundee reacts vigorously in acid, whereas in Well No. 10 it reacts very slowly. In Well No. 2 similar lithologic types are present at this contact but the brown granular Dundee rocks react less vigorously with acid than in Well No. 11, and more vigorously than in Well No. 10. Cavings from the Bell shale in samples above and below the Dundee-Detroit River contact in Well No. 2 obscure the lithologic change. The position of the contact with reference to the evaporites varies somewhat in the three wells. In Well No. 11 the contact is 25 feet above the first sample that contains abundant anhydrite; in Wells No. 10 and No. 2 it coincides with the first appearance of anhydrite in conspicuous quantity.

When all of the wells drilled to the Dundee in Manistee County and adjacent parts of neighboring counties are considered, the lithologic character of the formation in this part of Michigan is seen (Fig. 2) to be predominantly limestone. In only seven of the 40 wells on which information was available, does the Dundee consist entirely of dolomite. These are not grouped together but are interspersed with limestone wells. Five of the seven are located in the southwestern part of the area, where most of the wells have been drilled and therefore where we have the most information. Two other wells in this part of the area have dolomite and limestone in nearly equal proportions and three others contain some dolomite in the otherwise limestone Dundee.

Thickness of the Dundee

The recorded thickness of the Dundee limestone in Manistee County varies from 35 to 260 feet. The Isopach map (Fig. 3) is

DUNDEE LIMESTONE, MANISTEE COUNTY, MICHIGAN

THICKNESS OF THE DUNDEE LIMESTONE

ISOPACH INTERVAL 50 FEET

Fig. 3

TABLE I

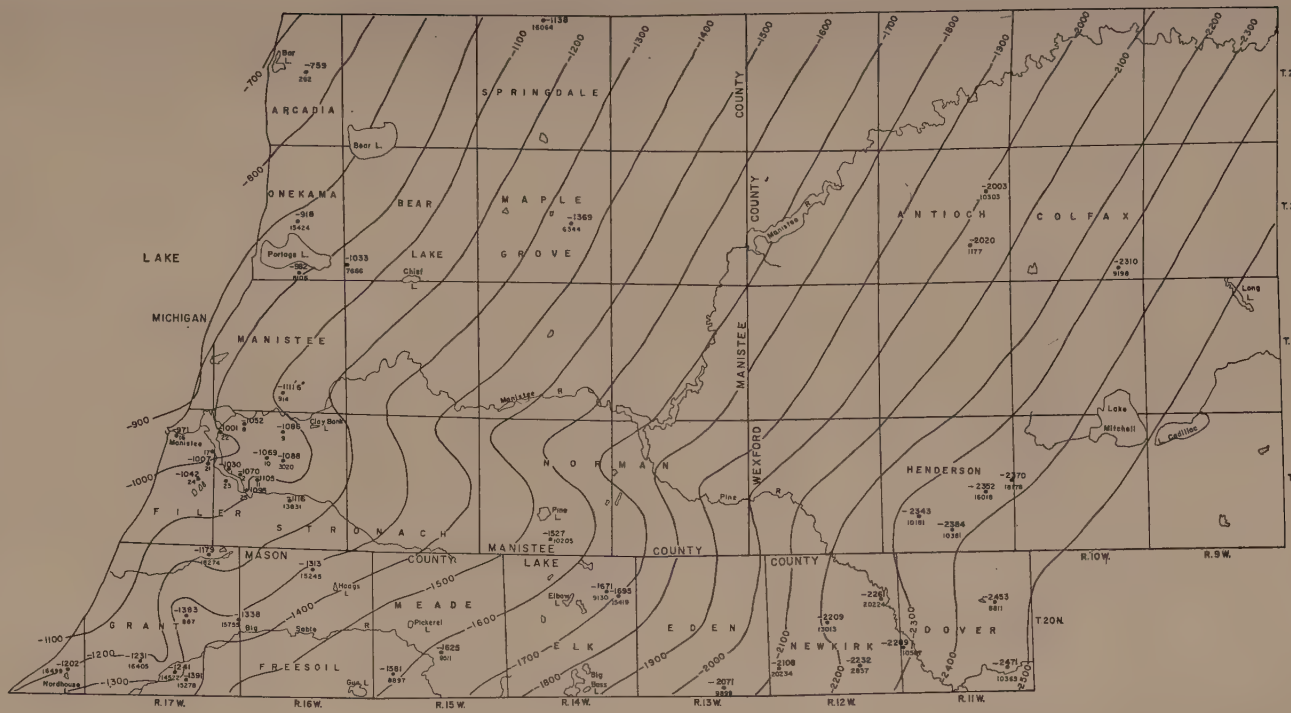
Map or permit number	Company	Well	Section	Township	Range	County	Name of township	Elevation in feet	Dundee Top		Thickness feet	Total depth feet	Production
									Depth in feet	Subsea elevation			
23	Great Lakes Chemical Corp.	Well No. 1	Sec. 19	21N	16W	Manistee	Filer	?	1665		35′	2513	Brine well
16		Canfield-Wheeler Well	NW¼ Sec. 11	21N	17W	Manistee	Filer	604	1575	− 971	80′	1947	Dry hole
21	Morton Salt Co.	No. 2-C (Drilled Dec., 1938 to May, 1939)	SE¼ SW¼ NE¼ Sec. 13	21N	17W	Manistee	Filer	663	1670	−1007	35′	2529	Brine well
24	Great Lakes Chemical Corp.	Well No. 4	SW¼ NE¼ NW¼ Sec. 24	21N	17W	Manistee	Filer	658	1700	−1042	150′	2565	Brine well
22	R. G. Peters Salt & Lumber Co.	Well No. 7	NW¼ NW¼ Sec. 7	21N	16W	Manistee	Manistee	594	1595	−1001	25′	2390	Salt well
9	Standard Lime and Cement Co.	Well No. 9	SW¼ SW¼ SW¼ Sec. 3	21N	16W	Manistee	Manistee	652.9	1739	−1086	86′	2692	Brine well
8	Standard Lime and Cement Co.	Well No. 8	NE¼ NW¼ SE¼ Sec. 5	21N	16W	Manistee	Manistee	593	1645	−1052	71′	2516	Brine well
17	Ruggles & Rademaker	Well No. 25 (Drilled in 1927)	SE¼ SE¼ Sec. 12	21N	17W	Manistee	Manistee	?	1597		133′	2012	Salt well
914	Swastika Oil and Gas Co.	W. H. Cromer No. 1	NW¼ NW¼ Sec. 34	22N	16W	Manistee	Manistee	615	1726′6″	−1111′6″	113′6″	2060	Dry hole
3020	Royalcase, Inc.	Red Wing Development Co. No. 1	NW¼ NW¼ NW¼ Sec. 15	21N	16W	Manistee	Stronach	684.6	1773	−1088	52′	2188	Dry hole
25	Great Lakes Chemical Corp.	Well No. 5	C E½ NE¼ SW¼ Sec. 20	21N	16W	Manistee	Stronach	601	1696	−1095	260′	2625	Brine well
13831	Byron MacCallum	Sands Lumber Co. No. 1	SE¼ SE¼ SW¼ Sec. 22	21N	16W	Manistee	Stronach	672.1	1788	−1116	50′	2100	Dry hole
1	Standard Lime and Stone Co.	Well No. 1	NW¼ SE¼ Sec. 18	21N	16W	Manistee	Stronach	600	1630	−1030	80′	2598	Brine well
2	Standard Lime and Stone Co.	Well No. 2	SE¼ SW¼ SW¼ Sec. 17	21N	16W	Manistee	Stronach	670	1740	−1070	145′	2620	Brine well
10	Standard Lime and Cement Co.	Well No. 10	NE¼ NE¼ NW¼ Sec. 16	21N	16W	Manistee	Stronach	676.3	1745	−1069	135′	2670	Brine well
11	Standard Lime and Cement Co.	Well No. 11	NE¼ NE¼ NE¼ Sec. 20	21N	16W	Manistee	Stronach	674.4	1779	−1105	136′	2710	Brine well
10205	Franklin Petroleum Development Co.	C. A. Beebe No. 1	C N½ SW¼ NW¼ Sec. 34	21N	14W	Manistee	Norman	795.7	2323	−1527	95′	2628	Dry hole
15424	Angie Busk	Helen Bye No. 1	SE¼ SE¼ NE¼ Sec. 22	23N	16W	Manistee	Onekama	742.1	1660	− 918	?	1671	Dry hole
8106	Willliam P. Shoemaker	N. & K. Rogers No. 1	C S½ NE¼ SE¼ Sec. 34	23N	16W	Manistee	Onekama	595	1577	− 982	81′	2588	Dry hole

7666	E. W. Collins & Wm. P. Shoemaker	Louis C. Schimke No. 1		NW¼ SW¼ NW¼ Sec. 31	23N	15W	Manistee	Bear Lake	626.5	1660	−1033	?	1676	Dry hole
6344	Maple Grove Oil Drilling Co.	H. & A. Niukkala No. 1		SE¼ NW¼ NW¼ Sec. 23	23N	14W	Manistee	Maple Grove	768.3	2137	−1369	?	2179	Dry hole
282	Fisher Robbins Oil & Gas Co.	Chamberlain Estate		SW¼ NE¼ SW¼ Sec. 14	24N	16W	Manistee	Arcadia	602	1361	− 759	?	1362	Dry hole
16064	Mercer Oil Co., Inc.	State-Springdale No. 1		SE¼ NE¼ NE¼ Sec. 4	24N	14W	Manistee	Springdale	766.5	1905	−1138	55′	2803	Dry hole
1177	Cummer-Diggins Co.	Cummer-Diggins No. 1		SW¼ NW¼ Sec. 26	23N	11W	Wexford	Antioch	1160	3180	−2020	105′	3860	Dry hole
10303	Ranch Oil Co.	L. Browning et al No. 1	C	S½ SE¼ SE¼ Sec. 11	23N	11W	Wexford	Antioch	1042.9	3046	−2003	114′	3210	Dry hole
9198	Shakespare Associates	City of Cadillac No. 1	C	W½ SE¼ NE¼ Sec. 35	23N	10W	Wexford	Colfax	1465.4	3775	−2310	73′	3917	Dry hole
18179	Sun Oil Co.	Russell Ridgeway No. 1		SE¼ SE¼ SE¼ Sec. 13	21N	11W	Wexford	Henderson	1317.7	3688	−2370	88′	3919	Dry hole
16018	Sun Oil Co.	State-Henderson No. 1		SE¼ SW¼ NE¼ Sec. 23	21N	11W	Wexford	Henderson	1348.4	3700	−2352	85′3″	5130	Dry hole
10181	Midwest Refineries, Inc.	George Wait No. 1	C	S½ SW¼ NE¼ Sec. 29	21N	11W	Wexford	Henderson	1108.8	3452	−2343	87′	3666	Dry hole
10381	Midwest Refineries, Inc.	Wm. L. Kellogg No. 1	C	N½ NW¼ NW¼ Sec. 34	21N	11W	Wexford	Henderson	1186	3570	−2384	82′	3795	Dry hole
9511	Gordon Oil Co.	Cartier Estate No. 2	C	S½ SW¼ SW¼ Sec. 22	20N	15W	Mason	Meade	705.5	2331	−1625	75′	2459	Dry hole
8897	Gordon Oil Co.	Cartier No. 1		SE¼ SE¼ SE¼ Sec. 30	20N	15W	Mason	Meade	730.5	2312	−1581	68′	3256	Dry hole
15245	Dow Chemical Co.	J. Chlebaski No. 1		SW¼ SE¼ SW¼ Sec. 3	20N	16W	Mason	Freesoil	707	2020	−1313	70′	2985	Dry hole
18274	Angie Busk & Carl E. Grimes	Joseph Pagans No. 1		SW¼ SW¼ NE¼ Sec. 2	20N	17W	Mason	Grant	668.4	1847	−1179	52′	1951	Dry hole
15755	Robert Bond	Donald Cameron No. 1		SE¼ NE¼ SE¼ Sec. 13	20N	17W	Mason	Grant	670	2008	−1338	92′	2216	Dry hole
887	Diamond-Thompson-Holland	Lewis No. 1		NW¼ NW¼ SE¼ Sec. 15	20N	17W	Mason	Grant	652	2035	−1383	125′	2380	Dry hole
14522	Louis Rose	James F. Goodrich No. 1		SW¼ SW¼ SW¼ Sec. 27	20N	17W	Mason	Grant	618.6	1860	−1241	121′	1981	Dry hole
16405	Dow Chemical Co.	Carnagel Trust No. 1		NE¼ NE¼ SW¼ Sec. 29	20N	17W	Mason	Grant	656.4	1887	−1231	118′	2758	Dry hole
15278	Louis Rose	G. Rakoski No. 1		NW¼ SW¼ NE¼ Sec. 34	20N	17W	Mason	Grant	653.6	2045	−1391	48′	2149	Dry hole
16499	Dow Chemical Co.	Eleaze B. Reed No. A-1		SE¼ SW¼ SW¼ Sec. 26	20N	18W	Mason	Grant	638.1	1840	−1202	67′	2641	Dry hole
15419	W. B. Darke	E. P. Felton No. 1		NE¼ NW¼ SW¼ Sec. 12	20N	14W	Lake	Elk	850.4	2545	−1695	94′	2702	Dry hole
9130	Ohio Oil Co.	Guy Fairbanks No. 1	C	S½ SW¼ NE¼ Sec. 11	20N	14W	Lake	Elk	852.4	2523	−1671	136′	3938	Dry hole
9899	Charles W. Teater	Marion Allen No. 1	C	E½ NE¼ SE¼ Sec. 34	20N	13W	Lake	Eden	925.6	2997	−2071	88′	3195	Dry hole
20234	Ace Oil Co.	State-Newkirk No. 1		SE¼ SE¼ SW¼ Sec. 30	20N	12W	Lake	Newkirk	980	3088	−2108	91′	3238	Dry hole
2837	Charles W. Teater	McCabe Estate No. 1		NE¼ SW¼ SW¼ Sec. 26	20N	12W	Lake	Newkirk	1054	3286	−2232	84′	3500	Dry hole
13013	C. E. Weller	State-Newkirk No. 1		SE¼ SW¼ SE¼ Sec. 16	20N	12W	Lake	Newkirk	949.5	3159	−2209	148′	3487	Dry hole
20224	Swanson Consolidated Oil Co.	State-Newkirk No. 1		SW¼ SW¼ SW¼ Sec. 12	20N	12W	Lake	Newkirk	992.4	3253	−2261	192′	3445	Dry hole
10365	Charles W. Teater	E. E. & D. Heyd No. 1	C	N½ NE¼ NE¼ Sec. 35	20N	11W	Lake	Dover	1135.3	3606	−2471	82′	3797	Dry hole
10587	C. L. Maguire, Inc.	B. Choponis No. 1		NW¼ NW¼ NW¼ Sec. 30	20N	11W	Lake	Dover	1091.3	3380	−2289	70′	3578	Dry hole
8811	Vorhees Drilling Co.	W. L. Kellogg, U. S. Government-Fee No. 1	C	NE¼ NW¼ Sec. 14	20N	11W	Lake	Dover	1262.3	3715	−2453	136′	3851	Dry hole

admittedly based on inadequate data. It is suggestive rather than factual. Wells in the northern part of Mason and Lake counties and the western part of Wexford County furnished most of the control for the southern and eastern parts of Manistee County. Over most of northern and eastern Manistee County the thickness is under 100 feet. It thickens apparently eastward into Wexford County, reaching 105 feet in the Cummer-Diggins No. 1 well, and 114 feet in the Ranch Oil Co., L. Browning *et al.* No. 1 in Antioch Township. It thickens southward into northern Lake County attaining a thickness of 150 feet in the Ace Oil Co., State-Newkirk Well No. 1, and 192 feet in the Swanson Consolidated Oil Company, State-Newkirk Well No. 1 in Newkirk Township.

In southwestern Manistee County where the greatest number of wells have been drilled the Dundee limestone has both its thickest and its thinnest sections. At the south end of Manistee Lake the Great Lakes Chemical Co. well No. 5 records a thickness of 260 feet. A mile and a half to the northwest the same company's Well No. 1 records only 35 feet. Other nearby wells are the Standard Lime and Cement Company's Wells No. 2 and No. 11, which log 145 feet and 136 feet, respectively. The great variation in the recorded thickness of the formation in southwestern Manistee County and northwestern Mason County leads to considerable complexity of the isopachs in this area. The map shows five centers of rapid thickening of the Dundee limestone; four in Manistee County and one in Mason County. This apparent variation in thickness may be due in part to the fact that the contact between the Dundee and the Detroit River group is transitional in many wells. The top of the Detroit River group is placed where the evaporite series begins or where there is a change from limestone of the Dundee to dolomite of the Detroit River. It is therefore probable that the point selected as the top of the Detroit River may not be the same stratigraphic position in each well. Elsewhere in Michigan disconformities have been noted at the top and base of the Dundee formation, which may explain the variations in thickness.

The thickness of the Dundee as shown in Fig. 3 is much more complex than indicated by Cohee (1945, Fig. 2) in Manistee County on his isopach map of the state.



STRUCTURE CONTOUR MAP ON TOP OF THE DUNDEE LIMESTONE

FIG. 4

Structure

The structure contour map, Fig. 4, is based on data from 27 wells in Manistee County, 10 wells in Mason County, 12 wells in Lake County, and 7 wells in Wexford County. There is 1300 feet of structural relief on the top of the Dundee limestone in Manistee County. The regional dip is southeastward at the rate of about 41.6 feet per mile.

The well data for most of the county are meager. The only variation from the regional dip is in the southern tier of townships where a structural "nose" trends southeastward, continuing into Lake County. Wells Nos. 1, 2, 9, 10, and 11, studied by the writer, are located on this structural trend. On either side of it is a corresponding sag.

This structural picture of the Dundee limestone in Manistee County differs little from that shown by Cohee (1945, Fig. 1) on his contour map of the Dundee for the whole State.

Conclusions

This investigation has shown that the Dundee limestone is petroliferous in Manistee and adjoining counties. The formation is predominantly limestone, but limestone and dolomite are closely associated and in some wells the Dundee consists entirely of dolomite. In southwestern Manistee and northwestern Mason counties, where the wells are relatively close together, the Dundee appears to thicken and thin rapidly. This is probably explained in part by the transitional character of the contact between the Dundee and the Detroit River Group. Elevations on top of the Dundee limestone in wells now available confirm the presence of a gentle "nose" plunging southeastward toward the center of the Michigan Basin.

BIBLIOGRAPHY

Bassett, C. F. 1935. Stratigraphy and Paleontology of the Dundee Limestone of Southeastern Michigan. Geol. Soc. Amer., Bull., 46: 425–492.

Cohee, G. V., and L. B. Underwood. 1945. Lithology and Thickness of the Dundee Formation and the Rogers City Limestone in the Michigan Basin. U. S. Dept. Interior Geol. Survey, Oil and Gas Investigations, Preliminary Map 38.

Ehlers, G. M., E. C. Stumm, and R. V. Kesling. 1951. Devonian Rocks of Southeastern Michigan and Northwestern Ohio. Guidebook for the Stratigraphic

Field Trip of the Geological Society of America. Detroit Meeting, November 1951. Ann Arbor: Edwards Brothers, Inc.

Grabau, A. W., and W. H. Sherzer. 1910. The Monroe Formation of Southern Michigan and Adjoining Regions. Mich. Geol. and Biol. Survey, Publ. 2, Geol. Ser. 1, 1910. 248 pp., 32 pls., 9 figs.

Landes, K. K. 1951. Detroit River Group in the Michigan Basin. U. S. Dept. Interior, Geol. Survey Circ. 133. 23 pp., 12 figs.

MEDICINE

Papers of the Michigan Academy of Science, Arts, and Letters
Vol. XLIII, 1958 (1957 Meeting)

A COMPARISON OF ACETYLCHOLINE AND POTASSIUM CITRATE AS CARDIOPLEGIC AGENTS*

CARLOS MOTA, THOMAS GAHAGAN, AND CONRAD R. LAM
Henry Ford Hospital, Detroit, Michigan

Induced cardiac arrest is now a widely accepted principle in the surgery of intracardiac defects. With the heartbeat stopped, the surgeon can work precisely in a still and bloodless field within the heart, while the general body circulation is maintained by a mechanical pump-oxygenator. This experimental study was done to compare the efficiency and safety of the two cardioplegic agents, acetylcholine and potassium citrate.

In the initial studies of induced cardiac arrest, potassium chloride was used by Lam and associates (1) to stop the heart while the nervous system was protected by hypothermia. Because of a high incidence of ventricular fibrillation during the recovery phase, this group abandoned potassium chloride for acetylcholine induced arrest combined with the pump-oxygenator. The successful experimental use of this combination (2) has been recently confirmed in approximately 70 clinical cases of open heart surgery. A similar approach, using potassium citrate arrest as initiated by Melrose (3), has been used clinically by other workers (4).

In a series of 36 acute experiments the cardioplegic properties of acetylcholine and potassium citrate were compared. Eighteen experiments were done with each drug. There were 8 dogs in the acetylcholine series and 9 dogs in the potassium citrate series; from 1 to 4 experiments were performed on each animal. Through incisions in the right hemithorax, cannulae were inserted into the brachiocephalic artery and the superior and inferior venae cavae under ether-oxygen anesthesia. The cannulae carried the animal's blood to and from the pump-oxygenator when the animal's own heart and lungs were excluded from the circulation. A bubble oxygenator of the DeWall type combined with a Sigmamotor pump perfused the animal with flow rates averaging 50 cc. per kilo. per minute. After occluding the

* Supported by a grant from the Michigan Heart Association.

venae cavae to shunt all of the venous blood into the pump, the ascending aorta was clamped below the brachiocephalic cannula. Cardiac arrest was then produced by rapidly injecting the cardioplegic agent into the aorta below the clamp, where it promptly entered the coronary arteries. The acetylcholine dosage was 10 mg. per kilo. in a dilution of 10 cc. of physiological saline. Two cc. of a 25 per cent potassium citrate solution diluted to 20 cc. in whole heparinized blood was utilized according to the Melrose technique by rapidly injecting the mixture until arrest occurred. Usually between 10 and 15 cc. were needed. The hearts remained stopped for 10 minutes. Removal of the aortic clamp at that time allowed the inflow of oxygenated blood into the coronary arteries which started the heart. Pump-oxygenator perfusion continued until the heart had a coordinated rhythm and was able to support the circulation unaided. As no incision in the heart allowed the coronary perfusion to wash out the cardioplegic drug, a cannula was inserted via the azygos vein into the right atrium to drain off the coronary venous return until spontaneous heart action began. The drainage was analyzed for potassium to ascertain the rapidity and completeness of removal of the drug from the heart. The end point of recovery of the heart was determined by the return to a normal or near normal electrocardiogram and the presence of normal systemic blood pressure measured by an electronic manometer in the femoral artery. Approximately 20 minutes intervened between the conclusion of one experiment and the beginning of another on the same animal. In repeating the experiment on an individual animal the same cardioplegic agent was used as in the initial run.

Both acetylcholine and potassium citrate produced prompt and sustained cardiac arrest. There was a difference in the status of the heart during the arrest which could be seen in the electrocardiogram. The potassium-arrested heart usually exhibited a straight-line tracing with no electrical activity although occasional nondescript complexes occurred. The acetylcholine-arrested heart exhibited occasional small waves which appeared to be miniature P waves along with less frequent ventricular complexes. In addition, the acetylcholine-arrested heart responded to manipulation of the ventricular walls with small twitching contractions. Complete recovery followed arrest in all of the 18 experiments in which acetylcholine was used. Of the 18 experiments with potassium citrate, one heart did

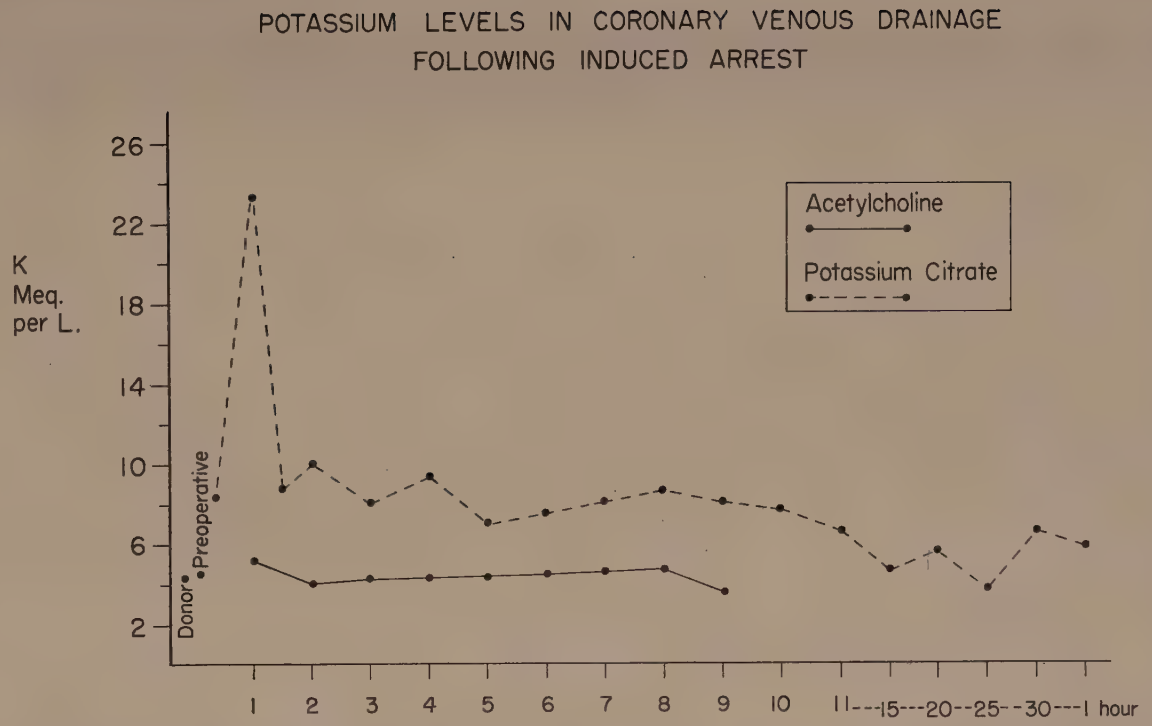


FIG. 1. Potassium values of coronary venous return during perfusion by pump-oxygenator following induced cardiac arrest by potassium citrate in 6 experiments and acetylcholine in 3 experiments. The mean values for blood potassium are plotted.

not recover. Ventricular fibrillation in this heart failed to respond to repeated electrical countershocks and 45 minutes of perfusion. Two other potassium-arrested hearts had ventricular fibrillation during the recovery period which responded promptly to countershock treatment. Four of the acetylcholine-arrested hearts also had ventricular fibrillation during the recovery period. In each of these instances a single countershock was sufficient to convert the rhythm to normal. Perfusion time needed for resuscitation following acetylcholine arrest averaged 10.2 minutes with 2 minutes being the shortest time required. Following potassium arrest, 12.8 minutes was the average perfusion time required, with 4 minutes the minimum. The amount of blood drained from the azygos vein varied somewhat with the length of the total perfusion time. This was not a factor in resuscitation, however, as the blood was replaced in equal amounts by transfusing the pump with fresh blood. Potassium levels in the coronary venous return following potassium-induced arrest rose to a mean level of 24 Meq. per liter in the initial minute of perfusion from a prearrest value of from 4 to 6 Meq. per liter. Within 2 to 3 minutes of perfusion, however, the potassium content of the coronary blood fell to normal levels as the original perfusate was removed from the system. Potassium determinations taken in the acetylcholine group as a control showed no deviation from normal during the perfusion (Fig. 1.).

Summary and Conclusions

In an experimental comparison of acetylcholine and potassium citrate, 1 of 18 potassium-arrested hearts did not recover because of ventricular fibrillation. Two other instances of ventricular fibrillation occurred in potassium-arrested hearts in which defibrillation was successful. Defibrillation was successful in the 4 acetylcholine-arrested hearts in which ventricular fibrillation occurred. None of the 18 hearts arrested with acetylcholine failed to recover. The mean perfusion time required in the acetylcholine group for recovery was 10.2 minutes, slightly shorter than the 12.8 minutes in the potassium group, with the one failure excluded.

LITERATURE CITED

1. Lam, C. R., Thomas Geoghegan, and Alfredo Lepore. 1955. Induced Cardiac Arrest for Intracardiac Surgical Procedures. Journ. Thoracic Surg., 30: 620.

2. Sergeant, C. K., Thomas Gahagan, and C. R. Lam. 1957. Further Studies in Induced Cardiac Arrest Using the Agent Acetylcholine. Surgical Forum of the American College of Surgeons, Vol. VII, Chicago.
3. Melrose, D. B., B. Dreyer, H. H. Bentall, and J. B. E. Baker. 1956. Elective Cardiac Arrest. Lancet, 2: 21.
4. Effler, D. B., L. K. Groves, F. M. Sones, and W. J. Kolff. 1956. Elective Cardiac Arrest in Open Heart Surgery. Cleveland Clinic Quarterly, 23: 105.

ZOOLOGY

Papers of the Michigan Academy of Science, Arts, and Letters
Vol. XLIII, 1958 (1957 Meeting)

SOME ECOLOGICAL OBSERVATIONS OF THE BIRDS OF SPRING, SUMMER, AND FALL ON 64 ACRES IN SOUTHERN MICHIGAN

H. LEWIS BATTS, JR.
Kalamazoo College, Kalamazoo, Michigan

Introduction

This study was undertaken in an attempt to determine populations and habitat relations of birds on the area during spring, summer, and fall, chiefly in respect to nesting sites, protection, food, and other vertebrates.

The area studied is a 64-acre portion of a 200-acre farm, the Newcomb Tract, owned by the University of Michigan. The tract is representative of various animal habitats on numerous farms in southern Michigan. The area is in the northwest portion of Section 6, Webster Township (T. 1 S.; R. 5 E.), Washtenaw County, Michigan, approximately 12 miles northwest of the Ann Arbor campus of the University and six miles north of Dexter, Michigan.

Seven principal habitats were determined as follows: Open Water, Marsh, Woods, Woodslope, Fencerow, Alpha Field, and Beta Field.

In order to establish more accurately the boundaries of the habitats and to be able to locate rather precisely any point on the area, the 64-acre tract was marked off in grid form (Pettingill, 1946, p. 200). The eastern border of the area is a mid-section line, and was chosen as the north-south base line for determining the square-acre grid. The grid corners were indicated by markers in the field.

In censusing the bird population these grid lines were traversed systematically. All censuses were begun at approximately the same time of day, early morning, and individual birds were plotted on maps in the field. Also, the time allotted to each census was constant relative to the seasons.

The study period included three spring seasons, three summers, and a fraction more than two fall seasons of bird censusing. Ninety almost weekly censuses were taken on the area during this period, involving about 451 hours of field observation. The first census taken was on November 19, 1947, and the last was on August 17,

1950. An additional 1444 hours were spent in field observation of nesting, habitat relationships, etc., for this project.

A limited amount of color-banding was carried out as an aid in identifying the nesting birds. The area was searched systematically for nests acre by acre. Each nest was located on a grid map in the field, as were the birds observed during each census. Field notes and the census maps supply the data from which this paper is compiled.

Amphibians and reptiles were recorded only incidentally with other phases of the study. Mammals were purposely trapped, or were caught incidentally during bird-banding operations, or were noted in the course of the field observations. Twenty-six species of mammals were identified on the study area.

Acknowledgment is made here with gratitude to Drs. William H. Burt, Frank E. Eggleton, Frederick H. Test, and the late Carl D. LaRue for a critical reading of the thesis from which this paper is taken, and especially to Dr. Harry W. Hann for his many valuable suggestions in every phase of the study.

Description of Study Area

The physiography, soils, and vegetation of the area and its habitats have been previously described (Batts, 1957). However, additional observations on the climate and habitats during the seasons concerned are included in the present paper.

The climate of this vicinity is characterized by fairly cold winters and warm summers, with a mean annual temperature of 47.5°F. Temperature and total precipitation data for the entire study period (recorded at the Willow Run Airport Weather Station approximately 27 miles southeast of the Newcomb Tract) were as follows:

Year	Spring		Summer		Fall	
	temp. °F	ppt. in.	temp. °F	ppt. in.	temp. °F	ppt. in.
1947					54.37	7.59
1948	47.93	10.65	71.80	7.18	53.83	7.78
1949	48.27	7.52	74.37	10.52	51.43	7.64
1950	43.87	10.72	69.60	8.15		

In this study the seasons are considered to be as follows: Spring—March, April, May; Summer—June, July, August; Fall—September,

October, November. The average length of the frost-free season is 165 days (May 2 to October 13, inclusive). The mean annual precipitation, including melted snow, is 31 inches. The precipitation, however, is not a true indication of the actual amount of water on much of the lowland portion because of periodic flooding of this part, especially in the spring and early summer. Base Lake overflows its shore on the northeast side of the Newcomb Tract, and the water moves across the Marsh, Newcomb Lake, and much of the low Woods to the river.

The Marsh.—When the open Marsh is flooded by water seasonally, most of its vegetation is emergent or even submerged. These periods of high water lasted as long as two months during the spring period in 1948 (March 20 to May 27), and one month during the summer period in 1950 (June 15 to July 19). On April 5, 1949, the water reached its maximal observed depth in this habitat—four feet. Apparently the animal populations are strongly influenced by these rather sudden inundations of their nesting and/or feeding places. There were even a number of spawning carp here in late May.

The red-winged blackbird, yellow warbler, yellow-throat, Traill's flycatcher, and swamp sparrow were characteristic nesting birds in the Marsh. The high water noticeably affected their nest sites, except for the yellow warbler, and influenced their nesting activities and success. The most active time of year for birds in the Marsh was during the breeding season when its plant and insect life were at their peak.

Other vertebrates of the Marsh are indicated in Table I. *Ondatra zibethica* and *Microtus pennsylvanicus* were the most obviously characteristic vertebrates of the Marsh; they and their activities were observed there throughout the year.

The Woods.—Seasonal floods in the Woods are due to the rise of water in Base Lake and are similar to those described for the Marsh. However, the Woods is completely inundated for a shorter period than the Marsh because of its slightly greater elevation. Pools of water in diminishing size and number remained in the Woods throughout much of the summer. In 1948, small pools remained until about the middle of August, and the soil was quite moist until the middle of September, but in 1949 the Woods was dry by early July. On April 5, 1950, a maximum depth of two feet of water was observed, but all standing water was gone by the first week in August.

TABLE I

AMPHIBIANS, REPTILES, AND MAMMALS BY HABITATS

Species	Open Water	Marsh	Woods	Wood-slope	Fence-row	Alpha Field	Beta Field
Amphibians							
Ambystoma tigrinum	*	*					
Bufo terrestris		*	*	*	*	*	*
Acris crepitans		*	*				
Pseudacris nigrita		*	*				
Hyla crucifer		*	*				
Hyla versicolor		*	*				
Rana catesbeiana	*	*					
Rana clamitans	*	*	*				
Rana pipiens	*	*	*				
Rana sylvatica		*	*				
Reptiles							
Sternotherus odoratus	*	*					
Chelydra serpentina		*		*		*	
Emys blandingii		*					*
Graptemys geographica				*		*	
Chrysemys picta	*	*		*		*	
Coluber constrictor	*	*		*	*	*	*
Storeria dekayi						*	
Thamnophis butleri		*					
Thamnophis sauritus		*					
Thamnophis sirtalis		*		*	*	*	*
Mammals							
Didelphis virginiana					*	*	
Scalopus aquaticus				*	*	*	*
Sorex cinereus				*			
Blarina brevicauda				*		*	
Eptesicus fuscus		*		*		*	
Procyon lotor		*	*	*	*	*	
Mustela erminea		*		*			
Mustela frenata				*			
Mephitis mephitis					*	*	
Canis familiaris				*	*	*	*
Vulpes fulva				*		*	
Felis domesticus				*	*	*	*
Marmota monax			*	*	*	*	
Citellus tridecemlineatus					*	*	*
Tamias striatus				*	*		
Tamiasciurus hudsonicus				*	*		

TABLE I—(*Continued*)

Species	Open Water	Marsh	Woods	Wood-slope	Fence-row	Alpha Field	Beta Field
Sciurus carolinensis...			*	*			
Sciurus niger.....				*			
Glaucomys volans.....				*			
Peromyscus manicula-tus.....			*	*		*	
Peromyscus leucopus...		*	*	*		*	
Synaptomys cooperi....		*					
Microtus pennsylvani-cus.....		*					
Ondatra zibethica.....	*	*					
Zapus hudsonius.....						*	
Sylvilagus floridanus...		*	*	*	*	*	*

The downy woodpecker, black-capped chickadee, white-breasted nuthatch, and common starling are characteristic nesting birds in the Woods. None of their nest sites were affected directly by the periodic rise of water, though apparently the high water provided the numerous potential sites by killing some of the trees.

Other vertebrates of the Woods are indicated in Table I.

The most commonly observed mammal was *Sciurus carolinensis*, which definitely affected the bird population adversely by its presence. *Procyon lotor* was observed in a den tree several times, as well as moving about on the ground.

The Woodslope.—A small portion of the Woodslope reaches out into the Marsh in a fingerlike peninsula, three to five feet above the surrounding marshland. Only once, on April 5, 1950, was the flood water, commonly found in the Marsh and Woods, observed over this peninsula in any appreciable amount; it was about one foot deep and moving swiftly.

The warbling vireo and eastern towhee are characteristic nesting birds in the Woodslope. During the migration seasons, bird movement seems to follow this wooded strip along both the river and lake shores. The area affords food and also shelter from the winds that sweep the more open areas.

The Fencerow.—The indigo bunting was the most characteristic nesting bird in this habitat, but others such as catbird, cardinal,

chipping sparrow, and song sparrow commonly used it for their nesting sites. Other vertebrates observed in the Fencerow are indicated in Table I.

The Alpha Field.—The most characteristic nesting bird of the Alpha Field was the field sparrow. Often the chipping sparrow nested in the small junipers, and the song sparrow nested on the ground in this habitat. In winter the field was practically deserted since it was not open enough for horned larks, and perhaps too open for other birds except an occasional junco, chickadee, or pheasant. Other vertebrates of the Alpha Field are indicated in Table I.

The Beta Field.—When cattle no longer used the Beta Field for a pasture, its vegetation and bird life changed noticeably. With cattle there in 1948, no birds nested. The cattle were removed from the field early enough in 1949 for the horned larks to nest there. In the summer of 1949, four pairs of vesper sparrows and one pair of grasshopper sparrows were present along with one pair each of bob-whites, field sparrows, and song sparrows. In 1950, the second year of unchecked growth of the vegetation, the vesper sparrow population dropped to two pairs, and the grasshopper sparrow population increased to three pairs. The field sparrow population remained at one pair in 1950, but the song sparrow did not nest there that year. This rather sudden change in the bird population both as to species and number of individuals is attributable for the most part to the rapid change in the vegetation from closely cropped plants to similar species from 2.0 to 3.5 feet high. Other vertebrates observed in the Beta Field are indicated in Table I.

Seasonal Changes

The three seasons of the study period present quite different aspects among the plant and animal communities in this general region. On the study area the seasons are characterized by the following observations:

In the spring bird migration results in an exodus of certain species, a redistribution of some, and an influx of others. A list of birds that were seen early during spring and/or fall on the area is given in the Checklist. Spring migration is accompanied and followed by a sudden rise in breeding activity among the birds, made possible in

part by the growing vegetation, which provides cover, nesting material, and food, and somewhat by an increase in insect availability at this same time. Spring, espccially the earlier part, is a period of adjustment from a rather stable winter population and its activities to a partly different breeding population of late spring and summer.

This season is typically one of renewed growth of vegetation and the awakening of dormant amphibians, reptiles, and certain mammals. This awakening is followed by breeding activity, especially noticeable among those amphibians that are vocal. Bird song also is much more evident in spring and early summer.

The transition from spring to summer is gradual and less noticeable on the area than the other seasonal changes. This period, as mentioned before, is the chief time of high water on the lowland portions, and the effects of this upon plants and animals are quite evident.

Summer is the period of luxuriant plant growth accompanied by a peak in animal populations due to production of young throughout the area. However, this is the poorest time to observe their movements because of the abundant plant growth and the lessening of bird song. Grass and other herbaceous vegetation is waist-to-shoulder high in the lowland, and the Fencerow and edges of the Woods and Woodslope are densely overgrown. This vegetation provides abundant protection, nesting sites, nesting material, and also food, especially seeds, fleshy fruits, and associated insects.

Fall is characterized by a ripening of vegetation and the maturing of animal offspring produced earlier in the year. Birds and amphibians are much less vocal. Many birds are gathering in flocks and leaving or entering the area as part of the migration pattern.

Like spring, fall is a time of great fluctuation in animal population as to their diversity and number of both species and individuals. This is the transition period from the breeding season of population increase to the winter season of struggle for mere individual existence.

Birds of the Area

One hundred forty-nine species of birds were observed on the study area during spring, summer, and fall, and the following table summarizes their distribution seasonally:

Season	Number of Species	
Spring and/or fall only	57	
Spring only		25
Fall only		10
Spring and fall		22
Nesting on study area	54	
Summer birds not nesting	29	
Fall (also seen in winter)	1	
Spring (also seen in winter)	1	
Spring and fall (also seen in winter)	7	
Total	149	

The 9 most abundant nesting species in decreasing order of estimated number of pairs were as follows:

Catbird; song sparrow
American goldfinch
Field sparrow
Red-winged blackbird
Yellow warbler
Common yellow-throat
House wren
American robin

The 9 species whose nests were found most commonly were, in decreasing order, as follows:

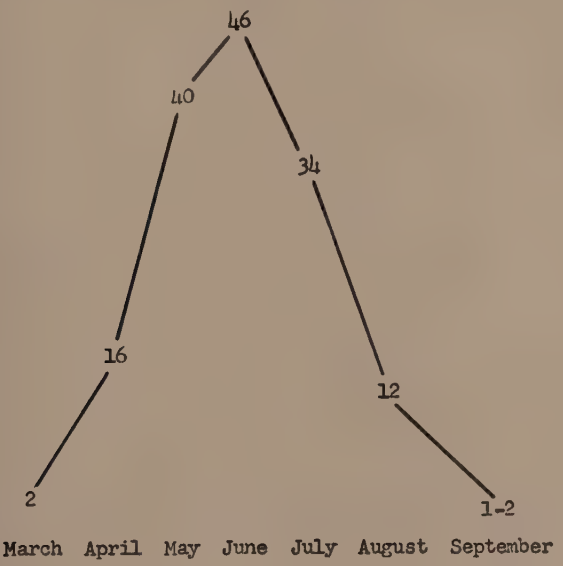
Catbird
Field sparrow
Red-winged blackbird; American goldfinch
Song sparrow
American robin; yellow warbler
House wren
Eastern bluebird

Discussion

During the spring, summer, and fall seasons the bird populations varied much in make-up, activity, and distribution throughout the various habitats. Of the 149 species of birds observed during this three-season period, 95 did not nest on the study area, and 54 nested there (see Checklist). Of the 95 non-nesting species, 52 (55 per cent) were transients; 29 (30.5 per cent) were summer residents; 11 (11.5 per cent) were permanent residents, and 3 (3 per cent) were winter residents. Of the 54 nesting species, 38 (70 per cent) were summer

residents, and 16 (30 per cent) were permanent residents. The main fluctuations in numbers of species and individuals were during the spring and fall migrations.

The nesting season on the study area extended from early in the last week of March to nearly the middle of September, with the peak in late May and early June, when early nesting overlapped late-nesting. Horned larks and bluebirds began nest construction during the early part of this period, and goldfinches still were fledging during the late part. The following graph shows the number of species nesting during each month of the nesting period:



Fluctuations during this season were primarily in number of individuals resulting from nesting (reproductive increases and accompanying losses) and from movements of the young onto and off the study area.

Spring.—The average population increased steadily in numbers of species and individuals from March through about the third week of May (Fig. 1). Populations of permanent resident species were the least altered during this period, and had little influence on the over-all population increase. However, seven species of permanent

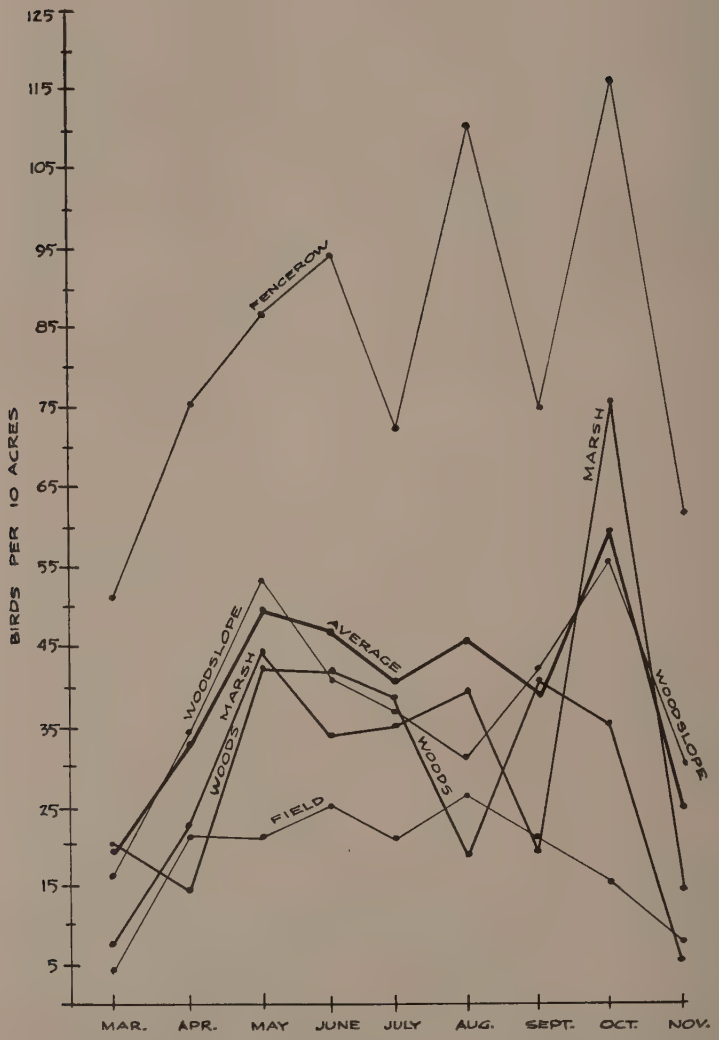


FIG. 1. Average monthly population density of birds by habitat in spring, summer, and fall, 1948–1950.

residents observed in spring did not nest on the study area; and one permanent resident, which nested during the summer, was absent from the area in spring (bob-white). In general, permanent residents merely modified existing winter territories at the breeding season and defended them more aggressively. They began nesting earlier than the summer residents, the earliest being the horned lark, which started nesting in March. Three winter resident species (purple finch, junco, tree sparrow) lingered on the study area into the spring season. Transient species made up the bulk of the migrating group and were most responsible for a sudden, though temporary increase in the bird population. They moved through and off the area rapidly, feeding on the way. Only 6 of the 43 transient species observed in the spring were seen at any time during the summer. The influx of summer residents has a more lasting effect upon the change in population from the winter condition to that of the summer. Thirty-seven of the 38 summer resident species nesting on the area arrived during the spring season; the Virginia rail was one not observed until summer. There were 28 other summer resident species present during spring which did not nest on the area during the study period. In general, the nesting summer residents spent the spring season setting up territories, chasing other birds, displaying, fighting, and nesting.

Summer.—The bird population of June, July, and August consisted of 54 nesting species, 16 non-nesting summer residents, 7 non-nesting permanent residents, and 6 transients. No winter residents were observed in summer. Some conflicts were witnessed, and some territories were shifted, but in general, this season was a more settled period than spring or fall, having less fluctuation in the make-up of the bird population. Evident fluctuations, however, in numbers of individuals resulted primarily from the addition of young produced by nesting birds on the study area or on adjacent areas. The peak of nesting was in late May and early June each year, and the largest summer population of breeding pairs of birds was in 1949 (Table III). The peak period in nesting was determined by an overlapping of early-nesting species and late nesters, and was increased especially by the subsequent nestings of earlier nesters.

Fall.—September through November was another period of adjustment from the more dynamic population of summer to the relatively more stable population of winter. Goldfinches still were

TABLE II

NUMBER OF SPECIES OBSERVED ON THE STUDY AREA BY MONTH AND YEAR IN SPRING, SUMMER, FALL

	Spring									Summer								Fall						
	March			April			May			June			July			August		Sept.		Oct.		November		
	'48	'49	'50	'48	'49	'50	'48	'49	'50	'48	'49	'50	'48	'49	'50	'49	'50	'48	'49	'48	'49	'47	'48	'49
Tr	1	2	3	9	3	9	21	11	27				1	1		4		8	28	11	27	2	6	7
SR	22	13	23	51	38	44	97	97	129	92	102	119	80	96	88	56	71	30	58	21	37	2	2	13
PR	40	28	30	44	30	34	51	40	52	39	46	61	40	41	38	39	36	26	48	32	46	19	21	44
WR	9	4	2	4	3	6			1										2	3	8	2	5	6
Tot	72	47	58	108	74	93	169	148	209	131	148	180	121	138	126	99	107	64	136	67	118	25	34	70

Tr Transient
SR Summer resident
PR Permanent resident
WR Winter resident
Tot Total

fledging in September, but the general nesting season was over on the study area by that time. There was considerable movement onto, throughout, and off the area in the fall. Bird families and flocks of immature birds were chiefly responsible for the fluctuations early in the fall season, but transients and large flocks of adults and immatures contributed to the fluctuations later. Also there was some reshuffling of the permanent resident population on the area. Eight non-nesting permanent residents and 3 winter residents invaded the area during the fall; and 26 nesting and 11 non-nesting summer resident species left the area during this season.

The Spring, Summer, Fall Period.—The average population fluctuation over the study period indicated a steady rise in numbers of species and individuals from March through its peak around the middle of May (Fig. 1), due primarily to the spring arrival of transients and summer residents. The decrease in number immediately following this peak was less marked than the increase which produced the peak. The decrease itself was mainly due to the departure of transients, and the larger remaining population resulted from the continued presence of summer residents. Another increase in the total average population was produced in the late summer by the accumulation of young birds. A decrease in the over-all population

followed in early fall when these young and some adults left the area. The average peak in October occurred as a result of the fall migration, when large numbers of transients and summer resident flocks invaded the area. The difference between the spring peak and the higher fall peak in total average population was due chiefly to the presence of birds of the year in the fall.

Although the foregoing general picture of spring-summer-fall population fluctuations was the average of the three years of observation, each year was different in population detail. In 1948, the coldest February of the three years was followed by the next-warmest March, which had the highest March population of any year of the study. This large March population was due to the lingering of a large number of winter resident species and a more continued bunching-up of permanent resident species on the area because of the cold. The following month in 1948 was the warmest April of the study period and had the highest April population. There were more summer and permanent residents on the area during April of the other two years. The next month was the coldest May and had the lowest May population of the period, in spite of the fact that it had the next-highest number of species. The yearly temperature variations of the months of June, July, and August apparently had little effect upon the bird populations during those months. However, September, 1948, the warmest September of the study period, had the lowest population for the month. Censuses showed that few transients were present, and no winter residents had invaded the area; also certain permanent residents had not yet begun their local wandering activity, which generally resulted in larger average numbers on the area. The following month was the coolest October and had the lowest October population of the study. If there was a fall peak in population numbers that year, the weekly censuses did not show it.

In 1949, the warmest February and March of the study period were followed by the next-warmest April and the warmest May. During this warm spring season the variations in the bird population due to the numbers of migrants (transients and summer residents) were spread out over a longer period of time in contrast to the sudden increase which followed a colder March and April during the following year in 1950. The actual peak in 1949 occurred in June, due to a continuous arrival of summer resident species and an increase in the number of permanent residents, especially from early nestings. The

fact that the May population was low in both transients and permanent residents further emphasized the size of the June population. The annual decrease in July was brought about by the temporary and/or permanent departure of summer residents. This was followed by an expected August population rise resulting from invasions of the area by flocks of young birds, occasionally mixed with adults, especially blackbirds. September, 1949, was the coolest September and had the highest average population density for the month. A larger number of summer residents and permanent residents were present on the area than during September, 1948. The following month had the highest October population of the study, due to continued influx of large numbers of individuals and flocks of summer residents in migration (especially blackbirds), and also to the arrival of winter residents following a cooler September.

March, 1950, following the next-coldest February of the three years, was the coldest March and had the lowest population density for the month, although not the smallest number of species (Table II). The summer resident population was smaller and only two winter resident species (junco, tree sparrow) were still present. The following month was the coldest April of the study and had the next-lowest population density for the month. With warmer weather in May the rise in population density was more abrupt than during the other two years, producing the highest May population density. An unusually large influx of summer residents in particular, along with a large number of transients, produced this sharp peak. The July slump and August rise in numbers of birds followed as in the previous years.

The chief fluctuations in bird populations on the study area from year to year during the spring-summer-fall season primarily were due to weather conditions, especially temperature. Migrants arrived early in the spring during a warm season and late during a cold season. A cold period in the midst of a warm spring slowed or stopped the migration movements, which were renewed with the return of warm weather. Temperature changes during the summer months, however, had little or no observed effect upon the resident population density. The year-to-year population variations during summer were traceable instead to the effect of precipitation (flooding) on ground nesters, to differences in reproductive increases and accompanying losses, and to differences in movements of bird families and

flocks of immatures onto and off the area. In the fall, however, a warm season resulted in a late migration, and a cold fall produced an early migration. Apparently the amount of food and its availability were fairly constant from year to year during the study, but there were critical periods in spring and fall when the food supply (especially insects) or its availability was probably inadequate to meet the bird's increased physiological demands resulting from lower temperatures (Kendeigh, 1934, p. 316).

Nesting Birds.—The 54 species of birds (38 summer residents and 16 permanent residents) nesting on the area during the study were distributed over the area by habitat and year as follows:

	Fence-row	Alpha Field	Beta Field	Wood-slope	Marsh	Woods	Entire Study Area
1948							
pairs/10 A.	36.67	13.09		15.54	29.90	23.31	15.91
no. species	8	9		14	15	19	41
1949							
pairs/10 A.	23.31	8.47	5.81	25.53	38.35	31.08	19.39
no. species	5	4	5	17	14	22	45
1950							
pairs/10 A.	39.96	11.55	6.65	22.20	29.90	23.31	17.98
no. species	10	7	5	17	14	17	46
Average							
pairs/10 A.	33.31	11.04	4.15	21.07	32.71	25.9	17.76
no. species	7.7	6.7	3.3	16	14.3	19.3	44

The *Fencerow* had the highest average population density of breeding birds. A relatively large number of species used it, although the small size of the habitat (three acres) probably affects statistical comparisons of population densities. The fact that in effect the Fencerow was all "edge" between other habitats also contributed to this high density. Birds nesting on the ground, in shrubs and vines, in open trees, or in cavities could and did find suitable nesting sites there which were available with little change during the study period, but the population densities did change. The densities of 1948 and 1950 were less different from each other than from the density of 1949. The over-all difference of 3.30 pairs per 10 acres (greater in

1950 than in 1948) was accounted for by the nesting of 2 more species in 1950, and by the redistribution of others. In 1949, fewer species nested in the Fencerow. Of the 12 different species nesting in this habitat during the study, only 3 nested there all three years (house wren, catbird, chipping sparrow). Shrubby undergrowth was the most-used niche for nest sites.

The *Alpha Field's* population density of breeding birds varied in pairs per 10 acres from 13.09 in 1948 to 8.47 in 1949, and to 11.55 in 1950, due almost entirely to changes in the number of species nesting in the habitat rather than to changes in the number of pairs nesting there from year to year. The field sparrow population, representing the most abundant species nesting in the Alpha Field, remained almost constant from year to year. The other two species nesting there each year were the goldfinch and chipping sparrow, the latter having a constant population throughout the three years. A total of 10 species nested in the Alpha Field during the study period. Suitable nesting sites were available each year for species nesting on the ground, in shrubby undergrowth, and in trees. Ground nesters were most abundant (especially field sparrows and song sparrows), and the scattered trees were used as nest sites only by robins and mourning doves. Although the vegetation increased considerably in density and general size during the three-year period, there was no noticeable change in nesting species traceable to this.

The breeding bird population density of the *Beta Field* varied from zero in 1948 to 5.81 pairs per 10 acres in 1949, and to 6.65 pairs per 10 acres in 1950. The absence of nesting birds in this habitat in 1949 was due to the activity of cattle grazing there. Species which later nested in the Beta Field were present and nesting on adjacent areas in 1948. Horned larks probably were kept out by the presence of the cattle themselves; whereas other species which nested there later (bob-white, meadowlark, grasshopper sparrow, vesper sparrow, field sparrow, and song sparrow) probably were unable to find suitable nest sites because of the closely cropped vegetation. At least three species moved into and nested in this habitat after the vegetation, mainly grass, was allowed to grow unchecked (1949–50). All nests were placed on the ground; the tallest plant was mullein (3–4 feet tall).

The *Woodslope* ranged in population density of breeding birds from a low of 15.54 pairs per 10 acres in 1948 to a high of 25.53 in

1949, then dropped to 22.20 in 1950. The increase from 1948 to 1949 was primarily due to an increase in the number of species from 14 to 17, although the wood pewee, catbird, and towhee increased in number of pairs considerably. Since the number of species nesting there in 1949 and 1950 was the same (17), the lower density in 1950 was the result of a redistribution of numbers of pairs, especially of house wrens, catbirds, and cardinals. Of the 22 species that nested in the woodslope during the study, 11 nested there each year. Of these 11, one was a ground nester exclusively (woodcock); another nested both on the ground and in the shrubby undergrowth (towhee); 3 consistently nested in the shrubby undergrowth (yellow-billed cuckoo, catbird, wood thrush); 3 nested high in trees (pewee, warbling vireo, Baltimore oriole); and 3 were cavity dwellers in natural or artificial sites (flicker, house wren, bluebird). The vegetation of the Woodslope changed but little over the three-year period, mostly a noticeable increase in size of the herbaceous and shrubby undergrowth along its edges at the Marsh and upland fields.

The average density of breeding birds in the *Marsh* was second to that in the Fencerow, but the number of species was nearly twice that of the Fencerow. The nesting density varied from a low of 29.90 pairs per 10 acres in 1948 and 1950 to a high of 38.35 in 1949. The number of species, however, remained almost constant. Of the 18 species nesting in the Marsh at some time during the study, 10 nested there each year. One nested on the ground exclusively (black duck); 2 that usually nested in the undergrowth also nested on the ground occasionally (yellow-throat, song sparrow); 6 others used the shrubs almost exclusively for nest sites (Traill's flycatcher, catbird, yellow warbler, red-wing, goldfinch, swamp sparrow); and one used both trees and shrubs, but mainly trees (kingbird).

In 1948, the Marsh was flooded by water in May, probably forcing the swamp sparrows to leave, and causing the black ducks to move to the Alpha Field where they re-nested in May. Nests of red-wings and song sparrows were also covered by water during this May flooding. High water in the early spring of 1948 and 1950 apparently resulted in population densities lower than that of 1949 when flooding did not occur until late in the nesting period.

The *Woods* habitat had a population density of 23.31 pairs per 10 acres in 1948 and 1950, and of 31.08 in 1949. The larger density was due to a considerable increase in the number of nesting pairs and

to an increase in the number of species. Of the 24 species nesting in the Woods during the three-year period, 12 nested there each year. Of these 12 species, none nested on the ground; only one utilized shrubby undergrowth for nest sites (wood thrush); 5 species nested openly in trees (pewee, robin, warbling vireo, Baltimore oriole, rose-breasted grosbeak); and the 6 others nested in natural cavities (flicker, hairy woodpecker, downy woodpecker, crested flycatcher, house wren, starling). The fluctuation in numbers of pairs and species nesting in the Woods was not indicative of a change in the vegetation of the habitat; apparently this habitat changed the least of any on the study area during the study period. The woodcock, a ground nester, attempted to nest in the Woods in 1948, but its nest with eggs was flooded by high water. Flooding was about the only noticeable variation in the habitat throughout the study, and this resulted in a decrease in the population of the Woods and an increase in the populations of the habitats where the woodcock moved to nest (Woodslope, Fencerow).

The average nesting population density of the *entire study area* increased by slightly less than 3.5 pairs per 10 acres from 1948 to 1949, then decreased by less than 1.5 pairs per 10 acres from 1949 to 1950. Of a total of 54 species nesting on the area during the study, 34 (25 summer residents and 9 permanent residents) nested there each year; 10 others (8 summer residents and 2 permanent residents) nested there in two of the three years; and 10 (5 summer residents and 5 permanent residents) nested there during only one year. The population density was lower in 1948 than in the other two years, due in part to the absence of nesting birds in the Beta Field and also to the early flooding of the Marsh, forcing out some nesting pairs. The presence of nesting birds in the Beta Field and the absence of high water in the lowland during the critical nesting period in 1949 accounted for the higher population density. Flooding of the Marsh occurred early during the nesting period again in 1950, and accounted for a part of the drop in population density that year. Also affecting the fluctuation in population density from year to year were the increases and decreases in number of species and individuals nesting on the area. Some species decreased in number or left entirely, others entered the area, and some already there increased in number —the interplay of decrease and increase resulting in the yearly fluctuation (Table III).

TABLE III

TOTAL AND AVERAGE POPULATION DENSITY OF BREEDING BIRDS IN PAIRS PER 10 ACRES OF NESTING HABITAT AND PER 100 ACRES OF STUDY AREA, 1948–1950

Species	1948		1949		1950		Average	
	Habitat	Study Area	Habitat	Study Area	Habitat	Study Area	Habitat	Study Area
Mallard			0.83	1.6	0.83	1.6	0.55	1.1
Black duck	0.83	3.1	0.83	1.6	0.83	1.6	0.83	2.2
Bob-white					0.83	1.6	0.28	0.5
Pheasant	0.83	1.6			0.83	1.6	0.55	1.1
Virginia rail	0.83	1.6					0.28	0.5
Woodcock	1.11	3.1	1.67	4.7	2.22	3.1	1.67	3.6
Spotted sandpiper	0.83	1.6					0.28	0.5
Mourning dove	0.94	3.1	1.11	1.6	2.05	3.1	1.36	2.6
Y-billed cuckoo	1.11	1.6	1.11	3.1	1.11	1.6	1.11	2.1
B-billed cuckoo			1.11	1.6	1.11	3.1	0.74	1.6
Hummingbird	1.11	1.6	1.11	1.6	1.11	1.6	1.11	1.6
Flicker	1.11	3.1	1.11	3.1	1.11	3.1	1.11	3.1
Hairy woodpecker	1.11	1.6	1.11	1.6	1.11	1.6	1.11	1.6
Downy woodpecker	2.22	3.1	1.11	1.6	1.11	1.6	1.48	2.1
Kingbird	1.67	3.1	1.67	3.1	1.67	3.1	1.67	3.1
Crested flycatcher	1.11	1.6	0.97	3.1	1.11	3.1	1.06	2.6
Traill's flycatcher	0.83	1.6	0.83	1.6	0.83	1.6	0.83	1.6
Wood pewee	1.11	3.1	1.67	4.7	1.11	3.1	1.30	3.6
Horned lark			0.83	1.6			0.28	0.5
Tree swallow	0.83	1.6	0.97	3.1	1.11	3.1	0.97	2.6
Blue jay					1.11	1.6	0.37	0.5
Crow			1.11	1.6			0.37	0.5
Chickadee	1.11	3.1	1.11	1.6	0.83	1.6	1.02	2.2
Tufted titmouse					1.11	1.6	0.37	0.5
W-breasted nuthatch	1.11	1.6	1.11	1.6			0.74	1.1
House wren	1.60	6.2	2.22	6.2	2.22	6.2	2.01	6.2
Catbird	2.60	14.0	2.57	12.5	2.83	10.9	2.67	12.5
Brown thrasher			1.11	1.6			0.37	0.5
Robin	1.74	4.7	2.22	6.2	1.67	4.7	1.88	5.2
Wood thrush	1.11	3.1	1.11	3.1	1.11	3.1	1.11	3.1
Bluebird	2.22	3.1	0.97	3.1	1.76	4.7	1.65	3.6
Cedar waxwing	1.11	1.6			3.33	1.6	1.48	1.1
Starling	2.22	3.1	4.44	6.2	3.33	4.7	3.33	4.7
Y-throated vireo			1.11	1.6			0.37	0.5
Red-eyed vireo	1.11	1.6	1.11	1.6			0.74	1.1
Warbling vireo	1.11	3.1	1.11	3.1	1.11	3.1	1.11	3.1

TABLE III—(*Continued*)

Species	1948		1949		1950		Average	
	Habitat	Study Area	Habitat	Study Area	Habitat	Study Area	Habitat	Study Area
Yellow warbler	3.32	6.2	7.47	14.0	2.49	4.7	4.43	8.3
Yellow-throat	3.32	6.2	4.15	7.8	3.32	6.2	3.60	6.7
Red-wing	4.15	7.8	5.81	10.9	4.15	7.8	4.70	8.8
E. meadowlark			0.77	1.6	0.83	1.6	0.53	1.1
Baltimore oriole	1.11	3.1	1.11	3.1	1.11	3.1	1.11	3.1
Cowbird		4.7		4.7		4.7		4.7
Scarlet tanager					1.11	1.6	0.37	0.5
Cardinal	3.89	4.7	3.33	4.7	3.89	4.7	3.70	4.7
R-breasted grosbeak	1.11	1.6	1.11	3.1	1.11	3.1	1.11	2.6
Indigo bunting	0.77	1.6			2.05	3.1	0.94	1.6
Goldfinch	2.85	10.9	3.73	12.5	3.68	14.0	3.42	12.5
E. towhee	2.22	3.1	2.22	3.1	2.78	4.7	2.41	3.6
Grasshopper sparrow			0.83	1.6	2.49	4.7	1.11	2.1
Vesper sparrow			2.49	4.7	1.67	3.1	1.39	2.6
Chipping sparrow	2.05	3.1	3.72	4.7	2.05	3.1	2.91	3.6
Field sparrow	4.62	9.2	2.73	10.9	3.11	12.5	3.49	10.9
Swamp sparrow	1.67	3.1	2.49	4.7	0.83	1.6	1.66	3.1
Song sparrow	3.82	12.5	3.88	12.5	3.26	12.5	3.65	12.5
Total Pairs		159.1		193.9		179.8		177.6
Total Species		41		45		46		54

Within the study area there was also a redistribution of breeding birds which did not necessarily affect the over-all population density of the area, but did affect the population densities of given habitats. For example, woodcock were flooded out of a nest site in the Woods, but then moved to another portion of the study area. Other nesting pairs moved from one habitat to another for various reasons. Since all habitat selection seemed to depend upon the presence of suitable nest sites, any considerable change in the availability of these sites effected a shift in the birds using them. For example, tree swallows nested in bird boxes in the Marsh until house wrens drove them out; then the swallows moved to natural cavities in trees along the edge of the woods at the shore of Base Lake. Changes in the vegetation itself also resulted in changes in the distribution of nesting pairs.

Literature

Population densities of breeding birds on areas similar to that of the present study have been reported in the literature less frequently perhaps than the changing conditions of the land and vegetation warrant. However, comparisons can be made with other studies involving many of the same bird species, or others occupying niches similar to those of the present study. In the following table the total average population density of the breeding birds on the study area, 177.6 pairs per 100 acres, is compared with densities determined elsewhere by various investigators (asterisk indicates figures changed to read in pairs per 100 acres).

Reference	Habitat, size, locality	Pairs/100 acres
Williams (1936)	65 acres beech-maple climax forest in northern Ohio	233* (ave.)
Kendeigh (1944)	8 acres of climax deciduous forest ranging in size from 14–65 acres (total 293 acres)	221 (ave.) 192–288 (range)
Erickson (1948)	82.48 acres of marsh and hammocks in eastern South Carolina	463
Young (1949)	5 acres of park land in southern Wisconsin	1,850*
Stewart *et al.* (1952)	2656 acres of woods and open country in central Maryland (Patuxent)	204
George (unpubl. thesis)	171 acres general farmland in southern Michigan (1948–50)	163.8 (ave.) 143.0–177.2 (range)
Present Study	58 acres (breeding habitats) (1948–50)	177.6 (ave.) 159.1–193.9 (range)

The differences among population densities of acres of different habitats and the similarity between those of similar areas studied at the same time (George, unpublished thesis, and present study) as shown in the table above, point out the need for studies such as the present one (covering longer periods of time on the same study areas) in order to get a more nearly accurate interpretation of natural populations and their changes. This plan eliminates many of the variables which cannot be weighed properly when comparing population densities of different habitats or of widely separated areas. Kendeigh

(1944, p. 88), in a discussion of the sizes of sample plots, and (*ibid.*, pp. 90–91) in a discussion of the frequency of observational surveys on the sample plots, suggests that high densities of nesting populations (as limited) were due to the small sizes of the sample areas, and that there are minimum frequency requirements. Such variables as these (statistical), as well as physical (climate, physiography) and biotic relationships (vegetation, predators), can be evaluated with greater validity when comparing changes in population densities, if they are observed on the same area over a long period of time. The provision of nest boxes, for example, on one area and not on another would probably be another source of error in making comparison habitat studies of nesting populations. Seven nest boxes on the study portion of the Newcomb Tract were used by 5 nesting species. These artificial sites probably had a favorable effect upon the size of the resident population of bluebirds, and perhaps of house wrens. However, the extent of this effect likely would not be comparable to that found in Kendeigh's house wren study (Kendeigh, 1944, p. 83).

Summary

1. A 64-acre portion of a southern Michigan farm was studied in an attempt to determine populations and habitat relations of birds found there during spring, summer, and fall. The study area is located approximately 12 miles northwest of the Ann Arbor campus of the University of Michigan. The study period began on October 16, 1947, and ended on August 17, 1950. During this period a minimum field observation time of 1895 hours was spent during spring, summer, and fall.

2. The study area was surveyed for physical conditions which included physiography, soils, geology, and seasonal climatic changes. The vegetation was surveyed and the area was divided and mapped into seven habitats as follows: Open Water, Marsh, Woods, Woodslope, Fencerow, Alpha Field, and Beta Field. Amphibians, reptiles, and mammals were noted as observed incidentally and as the result of limited systematic trapping.

3. Bird populations of spring, summer, and fall were determined by direct-observation and absolute-abundance methods. Ninety areal censuses were taken almost weekly throughout the study period. Maps showing habitats and a square-acre grid, whose corners were

marked in the field, were employed in the census-taking. Recorded notes concerning individual behavior of the birds involved in nesting activity, interspecific and intraspecific contacts, feeding, roosting, etc., were used along with the census maps as a basis for the discussion.

4. The bird population density of the spring-summer-fall period was characterized by a peak during migration in May and by a larger peak during migration in the fall due to the addition of birds of the year.

5. The nesting season on the study area extended from late March to the middle of September, with the peak in late May and early June.

6. Fluctuations during the nesting season were primarily in numbers of individuals resulting from nesting (reproductive increases and accompanying losses) and from movements of young onto and off the study area.

7. The chief fluctuations in bird populations on the study area from year to year during the spring and fall seasons were due primarily to weather conditions, especially temperature. Spring migration was earlier during a warm season and later during a cold season. Fall migration was earlier during a cold season and later during a warm season. Temperature changes during the summer, however, had little or no observed effect upon the resident population density.

8. A total of 54 species of birds (38 summer residents and 16 permanent residents) nested on the area during the study.

9. The Fencerow habitat had the highest average population density of breeding birds, 33.31 pairs per 10 acres, and the Beta Field had the lowest density, 4.15 pairs per 10 acres. The average for the entire study area for the three-year period was 17.76 pairs per 10 acres or 177.6 pairs per 100 acres.

Checklist of the Birds of the Study Area

PR–Permanent Resident
SR–Summer Resident
WR–Winter Resident
Tr–Transient Visitant
S–Spring
Su–Summer
F–Fall
*–Flying over area only

Species	Status	Nesting	Season Observed
Horned grebe, *Colymbus auritus*	Tr		S
Pied-billed grebe, *Podilymbus podiceps*	SR		S
Great blue heron, *Ardea herodias*	SR		S Su F
American egret, *Casmerodius albus*	Tr		S Su
Green heron, *Butorides virescens*	SR		S Su
Black-crowned night heron, *Nycticorax nycticorax*	Tr		Su
American bittern, *Botaurus lentiginosus*	SR		S Su
Canada goose, *Branta canadensis**	Tr		S F
Mallard, *Anas platyrhynchos*	SR	X	S Su F
Black duck, *Anas rubripes*	PR	X	S Su F
American widgeon, *Mareca americana*	Tr		S
Pintail, *Anas acuta*	Tr		F
Blue-winged teal, *Anas discors*	SR		S
Shoveller, *Spatula clypeata*	Tr		F
Wood duck, *Aix sponsa*	SR		S
Redhead, *Aythya americana*	Tr		S
Scaup ducks, *Aythya marila* and/or *Aythya affinis*	Tr		S
American golden-eye, *Bucephala clangula**	Tr		S
Buffle-head, *Bucephala albeola*	Tr		F
American merganser, *Mergus merganser*	Tr		S
Turkey vulture, *Cathartes aura*	SR		S Su F
Goshawk, *Accipiter gentilis**	Tr		S F
Sharp-shinned hawk, *Accipiter striatus*	Tr		S F
Cooper's hawk, *Accipiter cooperii*	PR		S Su F
Red-tailed hawk, *Buteo jamaicensis*	PR		S Su F
Red-shouldered hawk, *Buteo lineatus*	SR		S F
Broad-winged hawk, *Buteo platypterus*	Tr		S
Bald eagle, *Haliaeetus leucocephalus**	Tr		S
Marsh hawk, *Circus cyaneus*	PR		S Su F
Osprey, *Pandion haliaetus**	Tr		S F
Sparrow hawk, *Falco sparverius*	PR		F
Ruffed grouse, *Bonasa umbellus*	PR		S F
Bob-white, *Colinus virginianus*	PR	X	Su F
Ring-necked pheasant, *Phasianus colchicus*	PR	X	S Su F
Virginia rail, *Rallus limicola*	SR	X	Su
Killdeer, *Charadrius vociferus*	SR		S Su F
American woodcock, *Philohela minor*	SR	X	S Su F
Spotted sandpiper, *Actitis macularia*	SR	X	S Su
Herring gull, *Larus argentatus**	Tr		S F
Ring-billed gull, *Larus delawarensis**	Tr		S F

CHECKLIST OF THE BIRDS OF THE STUDY AREA—*Continued*

Species	Status	Nesting	Season Observed
Common tern, *Sterna hirundo**	Tr		S Su
Black tern, *Chlidonias niger*	SR		S Su
Mourning dove, *Zenaidura macroura*	SR	X	S Su F
Yellow-billed cuckoo, *Coccyzus americanus*	SR	X	S Su F
Black-billed cuckoo, *Coccyzus erythropthalmus*	SR	X	S Su
Barn owl, *Tyto alba*	PR(?)		F
Great horned owl, *Bubo virginianus*	PR		Su
Barred owl, *Strix varia*	PR		S
Whip-poor-will, *Caprimulgus vociferus*	SR(?)		S Su
Common nighthawk, *Chordeiles minor**	SR		S
Chimney swift, *Chaetura pelagica**	SR		S
Ruby-throated hummingbird, *Archilochus colubris*	SR	X	S Su
Belted kingfisher, *Megaceryle alcyon*	PR		S Su F
Yellow-shafted flicker, *Colaptes auratus*	PR	X	S Su F
Red-bellied woodpecker, *Centurus carolinus*	PR		Su
Red-headed woodpecker, *Melanerpes erythrocephalus*	SR		S
Yellow-bellied sapsucker, *Sphyrapicus varius*	Tr		S
Hairy woodpecker, *Dendrocopos villosus*	PR	X	S Su F
Downy woodpecker, *Dendrocopos pubescens*	PR	X	S Su F
Eastern kingbird, *Tyrannus tyrannus*	SR	X	S Su F
Crested flycatcher, *Myiarchus crinitus*	SR	X	S Su F
Eastern phoebe, *Sayornis phoebe*	SR		S Su F
Traill's flycatcher, *Empidonax traillii*	SR	X	S Su
Least flycatcher, *Empidonax minimus*	SR(?)		S
Eastern wood pewee, *Contopus virens*	SR	X	S Su F
Horned lark, *Eremophila alpestris*	PR	X	S Su
Tree swallow, *Iridoprocne bicolor*	SR	X	S Su F
Bank swallow, *Riparia riparia**	SR		S
Rough-winged swallow, *Stelgidopteryx ruficollis*	SR		S Su
Barn swallow, *Hirundo rustica*	SR		S Su F
Purple martin, *Progne subis*	SR		S Su F
Blue jay, *Cyanocitta cristata*	PR	X	S Su F
American crow, *Corvus brachyrhynchos*	PR	X	S Su F
Black-capped chickadee, *Parus atricapillus*	PR	X	S Su F
Tufted titmouse, *Parus bicolor*	PR	X	S Su F
White-breasted nuthatch, *Sitta carolinensis*	PR	X	S Su F
Red-breasted nuthatch, *Sitta canadensis*	Tr		S
Brown creeper, *Certhia familiaris*	Tr		S F
House wren, *Troglodytes aëdon*	SR	X	S Su F
Long-billed marsh wren, *Telmatodytes palustris*	SR		S

CHECKLIST OF THE BIRDS OF THE STUDY AREA—*Continued*

Species	Status	Nesting	Season Observed
Short-billed marsh wren, *Cistothorus platensis*	SR		F
Catbird, *Dumetella carolinensis*	SR	X	S Su F
Brown thrasher, *Toxostoma rufum*	SR	X	S Su F
American robin, *Turdus migratorius*	SR	X	S Su F
Wood thrush, *Hylocichla mustelina*	SR	X	S Su F
Hermit thrush, *Hylocichla guttata*	Tr		S F
Olive-backed thrush, *Hylocichla ustulata*	Tr		S F
Gray-cheeked thrush, *Hylocichla minima*	Tr		S F
Veery, *Hylocichla fuscescens*	Tr		S F
Eastern bluebird, *Sialia sialis*	SR	X	S Su F
Blue-gray gnatcatcher, *Polioptila caerulea*	SR		S Su
Golden-crowned kinglet, *Regulus satrapa*	Tr		S F
Ruby-crowned kinglet, *Regulus calendula*	Tr		S F
Water pipit, *Anthus spinoletta*	Tr		S
Cedar waxwing, *Bombycilla cedrorum*	SR	X	S Su F
Common starling, *Sturnus vulgaris*	PR	X	S Su F
Yellow-throated vireo, *Vireo flavifrons*	SR	X	S Su F
Red-eyed vireo, *Vireo olivaceus*	SR	X	S Su F
Warbling vireo, *Vireo gilvus*	SR	X	S Su F
Black and white warbler, *Mniotilta varia*	Tr-SR		S F
Golden-winged warbler, *Vermivora chrysoptera*	SR		S Su
Blue-winged warbler, *Vermivora pinus*	SR(?)		S
Tennessee warbler, *Vermivora peregrina*	Tr		S F
Nashville warbler, *Vermivora ruficapilla*	Tr		S F
Yellow warbler, *Dendroica petechia*	SR	X	S Su
Magnolia warbler, *Dendroica magnolia*	Tr		S F
Cape May warbler, *Dendroica tigrina*	Tr		F
Black-throated blue warbler, *Dendroica caerulescens*	Tr		F
Myrtle warbler, *Dendroica coronata*	Tr		S Su F
Black-throated green warbler, *Dendroica virens*	Tr		S F
Blackburnian warbler, *Dendroica fusca*	Tr		S F
Chestnut-sided warbler, *Dendroica pennsylvanica*	Tr		S Su F
Bay-breasted warbler, *Dendroica castanea*	Tr		F
Black-poll warbler, *Dendroica striata*	Tr		S F
Pine warbler, *Dendroica pinus*	Tr		F
Prairie warbler, *Dendroica discolor*	Tr		S
Palm warbler, *Dendroica palmarum*	Tr		S F
Oven-bird, *Seiurus aurocapillus*	SR		S F
Connecticut warbler, *Oporornis agalis*	Tr		S
Mourning warbler, *Oporornis philadelphia*	Tr		S

CHECKLIST OF THE BIRDS OF THE STUDY AREA—*Concluded*

Species	Status	Nesting	Season Observed
Common yellow-throat, *Geothlypis trichas*	SR	X	S Su F
Wilson's warbler, *Wilsonia pusilla*	Tr		S
Canada warbler, *Wilsonia canadensis*	Tr		S Su F
American redstart, *Setophaga ruticella*	SR		S Su F
House sparrow, *Passer domesticus*	PR		S Su F
Bobolink, *Dolichonyx oryzivorus*	SR		S Su
Eastern meadowlark, *Sturnella magna*	SR	X	S Su F
Red-winged blackbird, *Agelaius phoeniceus*	SR	X	S Su F
Baltimore oriole, *Icterus galbula*	SR	X	S Su
Rusty blackbird, *Euphagus carolinus*	Tr		S F
Purple grackle, *Quiscalus quiscula*	SR		S Su F
Brown-headed cowbird, *Molothrus ater*	SR	(X)	S Su F
Scarlet tanager, *Piranga olivacea*	SR	X	S Su
Cardinal, *Richmondena cardinalis*	PR	X	S Su F
Rose-breasted grosbeak, *Pheucticus ludovicianus*	SR	X	S Su
Indigo bunting, *Passerina cyanea*	SR	X	S Su
Evening grosbeak, *Hesperiphona vespertina*	Tr		S F
Purple finch, *Carpodacus purpureus*	WR		S F
Pine siskin, *Spinus pinus*	Tr		S
American goldfinch, *Spinus tristis*	PR	X	S Su F
Eastern towhee, *Pipilo erythrophthalmus*	SR	X	S Su F
Grasshopper sparrow, *Ammodramus savannarum*	SR	X	S Su
Vesper sparrow, *Pooecetes gramineus*	SR	X	S Su F
Lark sparrow, *Chondestes grammacus*	SR-Tr		F
Slate-colored junco, *Junco hyemalis*	WR		S F
American tree sparrow, *Spizella arborea*	WR		S F
Chipping sparrow, *Spizella passerina*	SR	X	S Su
Field sparrow, *Spizella pusilla*	SR	X	S Su F
White-crowned sparrow, *Zonotrichia leucophrys*	Tr		S F
White-throated sparrow, *Zonotrichia albicollis*	Tr		S F
Fox sparrow, *Passerella iliaca*	Tr		S F
Swamp sparrow, *Melospiza georgiana*	SR	X	S Su F
Song sparrow, *Melospiza melodia*	PR	X	S Su F
Lapland longspur, *Calcarius lapponicus*	Tr		S

LITERATURE CITED

Batts, H. Lewis, Jr. 1957. An Ecological Study of the Winter Birds of a 64-Acre Tract in Southern Michigan. Pap. Mich. Acad. Sci., Arts, and Letters, 42 (1956): 69–96.

Erickson, Arnold B. 1948. Passerine Bird Populations of the Savannah River Refuge, South Carolina. Auk, 65: 576–584.

George, John L. (1952). Birds of a Southern Michigan Farm. Unpublished Thesis, Submitted June, 1952, University of Michigan.

Kendeigh, S. Charles. 1934. The Role of Environment in the Life of Birds. Ecol. Mono., 4: 299–417.

—— 1944. Measurement of Bird Populations. Ecol. Mono., 14: 67–106.

Pettingill, Olin S., Jr. 1946. A Laboratory and Field Manual of Ornithology. Minneapolis: Burgess Pub. Co.

Stewart, Robert E., James B. Cope, C. S. Robbins, and John W. Frainerd. 1952. Seasonal Distribution of Bird Populations at the Patuxent Research Refuge. Am. Midl. Nat., 47: 257–363.

Williams, Arthur B. 1936. The Composition and Dynamics of a Beech-maple Climax Community. Ecol. Mono., 6: 318–408.

Young, Howard. 1949. A Comparative Study of Nesting Birds in a Five-acre Park. Wilson Bull., 61: 36–47.

Papers of the Michigan Academy of Science, Arts, and Letters
Vol. XLIII, 1958 (1957 Meeting)

BENTHIC ASSOCIATIONS OF SUGARLOAF LAKE

LEE D. BEATTY AND FRANK F. HOOPER
Ann Arbor, Michigan

Knowledge of the density and distribution of the animals and plants inhabiting a lake bottom is necessary before an appraisal can be made of benthic productivity. The objectives of this investigation were to learn (1) whether the littoral zone of Sugarloaf Lake, a shallow eutrophic Michigan lake, can be divided into biotic associations which should be sampled independently for productivity studies, and (2) if such assemblages are present, whether they can be associated with environmental differences.

The animal-plant associations of the littoral zone have been discussed frequently in the literature. Assemblages characteristic of specific habitats within the littoral zone have been discussed by Pennak (1940), Moffett (1943), Neel (1948), and Krecker and Lancaster (1933). Numerous other studies have dealt with the animals and plants at one or more collecting stations within the littoral zone (Eggleton, 1952; Andrews and Hasler, 1944; Brundin, 1949; Ball, 1948). The great effort expended in sorting and identifying the animals in bottom samples perhaps has discouraged intensive quantitative investigations and restricted the number of sampling sites established. The usual procedure is to select one or more transects passing through what appear to be typical portions of the lake bottom and to rely upon samples from points along these transects for estimates of conditions throughout the lake basin as a whole. Choice of transects and sampling sites is usually subjective, and depends upon the investigator's familiarity with the lake. The transect method was employed in a previous study of the benthic productivity of Sugarloaf Lake (Anderson and Hooper, 1956). Samples were collected at three stations along a transect extending from a point near shore to the lake's maximum depth. Bottom vegetation and soils along the transect appeared similar to those of large areas of the lake bottom. In general, monthly samples were similar in the kinds of animals present, and showed consistent population trends for some

species. Appearance of certain discrepancies in the counts of other species, however, led to the suspicion that the investigator failed to return to the same sampling location on successive months. Since the sampling stations were relocated each month by visual reference to shore points, deviation might be expected in the actual sampling site. The suspicion that considerable variability existed in what appeared to be uniform areas led to the present analysis of the entire lake bottom and its bottom fauna, flora, and soils.

Clearly, an appraisal of the homogeneity of a lake bottom is needed if the events in a lake basin as a whole are to be evaluated quantitatively. The discrete biological zones of the lake should be sampled as separate units. This procedure minimizes sampling variations and adds to the reliability of sampling data.

The definitions of littoral and sublittoral zones used here are those given by Eggleton (1931). The only area considered in this paper is the zone where aquatic vegetation is present (littoral). A small sublittoral area is present in the vicinity of station 15 where the basin is deeper than 12 feet.

Sampling Stations and Methods

Sugarloaf Lake, located in the northwestern part of Washtenaw County, has been the site of numerous studies in management of warm-water fish by the Institute for Fisheries Research. Many of the lake's limnological features have been discussed (Cooper, 1953; Hooper, 1956; Anderson and Hooper, 1956).

We took samples at 24 points in the lake. We located 22 sampling stations by superimposing a system of grid lines on a map of the lake. There was no conscious orientation by the investigator of the grid intersections on the map. Each grid intersection within the lake boundaries, except those less than 25 feet from shore, was used as a sampling station (Fig. 1). One station had to be abandoned because of its proximity to shore. We also took samples of bottom fauna at two points (stations A and B) which served for several years as regular monthly collecting sites (stations 1 and 2 of Anderson and Hooper, 1956). We completed sampling at 21 stations on November 23, 1955, and at the three remaining stations the following day. We made four hauls at each station with a modified Ekman dredge. This modification of the Ekman dredge for sampling a firm, shallow bottom has been described by Anderson and Hooper (1956). These authors

also described the procedures used in the present study for collecting, sieving, and sorting of benthos.

In addition to the four samples collected at each station for analysis of bottom fauna, one dredge sample was taken for soil analy-

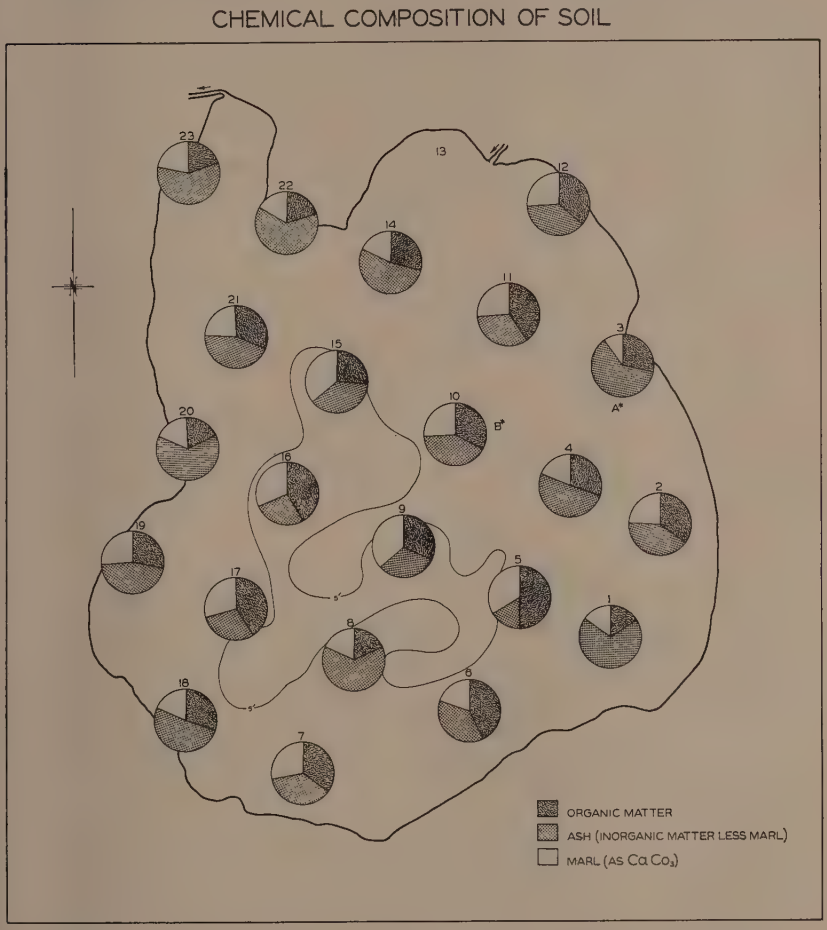


FIG. 1. Chemical composition of soil samples collected at 23 stations in Sugarloaf Lake on November 22, 1955. Identification numbers of the sampling stations are given immediately above the circles.

sis. An aliquot of each soil sample was oven-dried, weighed, and washed through a graded series of Tyler screens. Soil fractions retained by each screen were also dried and weighed. A second aliquot of each soil sample was oven-dried, weighed, and neutralized with 0.1 normal hydrochloric acid. The sample was then ashed in a muffle furnace and reweighed. From the amount of acid used to neutralize the soil, the marl content was calculated (as percentage calcium carbonate); and from the loss in weight by ashing, the quantity of organic matter in the sample was estimated. A quantity of calcium chloride equivalent to the calcium carbonate content of the original sample was subtracted from the ash weight. The difference was a measure of all inorganic substance except marl.

The modified Ekman dredge penetrates through materials on the mud surface, also collecting rooted aquatic plants. Hence the plants removed from the dredge haul provided a sample of the quantity and kind of vegetation at each station. After removing plant samples from the mud, we washed them in 0.1 normal hydrochloric acid to remove marl, dried them in an oven at 60° C., and weighed them on a sensitive balance.

Dr. LaVerne L. Curry, Central Michigan College, verified our identification of midges. R. O. Anderson and W. F. Hunter of the Institute for Fisheries Research staff assisted in collecting and analyzing bottom samples.

Morphometry and Soils

The basin of Sugarloaf Lake is saucer-shaped. From the water's edge, it slopes gradually for 50 to 100 feet. Beyond this point, the water is between three and four feet deep, and the bottom is essentially flat. The five-foot contour circumscribes a small, central depression (Fig. 1). The bottom of this depression is irregular and is broken up into several small subdepressions. The deepest of these (near station 15) has a depth of 20 feet. A second subdepression is in the vicinity of stations 5 and 9 (Fig. 1).

Soil particle size indicated that the bottom sediments were surprisingly uniform (Table I). At fifteen stations, from 35 to 55 per cent of the soil consisted of particles less than 0.147 millimeters in diameter. Particles of this size correspond to the very fine sand and silt categories of the U. S. Department of Agriculture textural classification. Sediments from only four stations contained over 10 per

TABLE I

PERCENTAGE OF BOTTOM SEDIMENT RETAINED BY SIEVES

Station number	Sieve aperture in millimeters				
	0.840	0.420	0.208	0.147	Less than* 0.147
1	7.2	8.2	27.7	12.8	44.1
2	15.5	15.7	20.2	8.2	40.3
3	4.4	13.7	19.8	9.8	52.2
4	6.5	24.6	23.5	6.8	38.6
5	0.5	4.6	8.6	3.4	82.9
6	12.2	5.7	43.3	13.4	25.4
7	4.2	17.9	31.7	12.1	34.1
8	0.5	23.3	25.1	7.6	43.5
9	51.3	9.9	10.4	5.4	23.0
10	0.4	20.5	20.0	9.2	49.8
11	0.6	22.0	23.0	8.2	46.2
12	0.9	13.9	22.3	7.8	55.2
14	0.6	16.8	22.0	9.7	50.8
15	1.5	14.1	19.2	12.1	53.2
16	11.1	14.0	18.9	10.2	45.9
17	1.5	16.3	27.4	9.0	45.8
18	0.2	24.5	19.0	9.8	46.5
19	0.5	3.6	18.1	15.9	61.8
20	0.4	11.7	30.0	20.3	37.6
21	0.4	25.5	17.9	8.5	47.7
22	6.2	9.8	52.4	22.6	9.1
23	0.2	18.0	19.2	2.1	60.5

* The percentage of sediment that passed through a sieve aperture of 0.147 millimeters.

cent of particles greater than 0.840 millimeters in diameter (coarse sand and gravel). Samples varied considerably in their percentage of soil particles greater than 0.42 millimeters in diameter. Much of the variation between stations in the quantity of larger sized particles was due to variable amounts of mollusc shell. The highest percentages of particles in the intermediate size ranges (0.42–0.147 millimeters) were to be found where the bottom was firm (stations 1, 6, 7, 20, and 22). The silt fraction was highest in the shallow embayments on the windward side of the lake (stations 19 and 23) and at station 5.

Chemical properties of the soils also showed considerable uni-

formity (Fig. 1). The marl content varied between 11 and 38 per cent. It was highest near the central depression (stations 5, 9, and 15) and lowest where the bottom was firm (stations 3, 20, and 22). Ash content tended to be highest at the shallowest depths and on the more exposed shores (stations 1, 3, 20, 22, and 23). Sediments at station 8 had a high ash content although records showed that benthos samples were taken at depths of 4.5 to 5 feet. We think that the soil sample for station 8 was taken a short distance from the bottom-sampling site, on a projecting sand spit, where the water is between 3 and 4 feet deep. This sample therefore is probably not representative of conditions at the benthos-collecting site.

The organic content of the sediments varied between 16 and 50 per cent. The lowest values occurred at the more exposed or shallow stations (1, 20, 22, and 23). The organic content, however, was not appreciably greater in the central depression than at depths of three to five feet.

Ash content appeared to be the most diagnostic of the soil measurements. It separated the compact bottom at stations on exposed shores in very shallow water from the bottom types at other stations. Particle size, marl content, and organic content were more variable measurements because they were strongly influenced by local concentrations of plant detritus and mollusc shells.

Vegetation

The stonewort *Chara* was the predominant submerged plant, constituting at least 95 per cent of the vegetation at 17 of the 23 sampling stations (Fig. 2). At five of the remaining stations there was an association of *Najas* and *Potamogeton*. *Najas* was predominant in sheltered bays (stations 12 and 18), and *Potamogeton* predominated in the central depression (stations 9, 15, and 16). At one station (22), there was a sparse stand of *Cyara* and *Najas*, with a trace of *Potamogeton*.

Sampling and visual observation indicated that there were no dense stands of *Chara*. Samples from the *Chara* zones averaged only 1.83 grams dry weight per one-quarter square foot. By contrast, samples from the *Najas-Potamogeton* beds averaged 5.88 grams per one-quarter square foot.

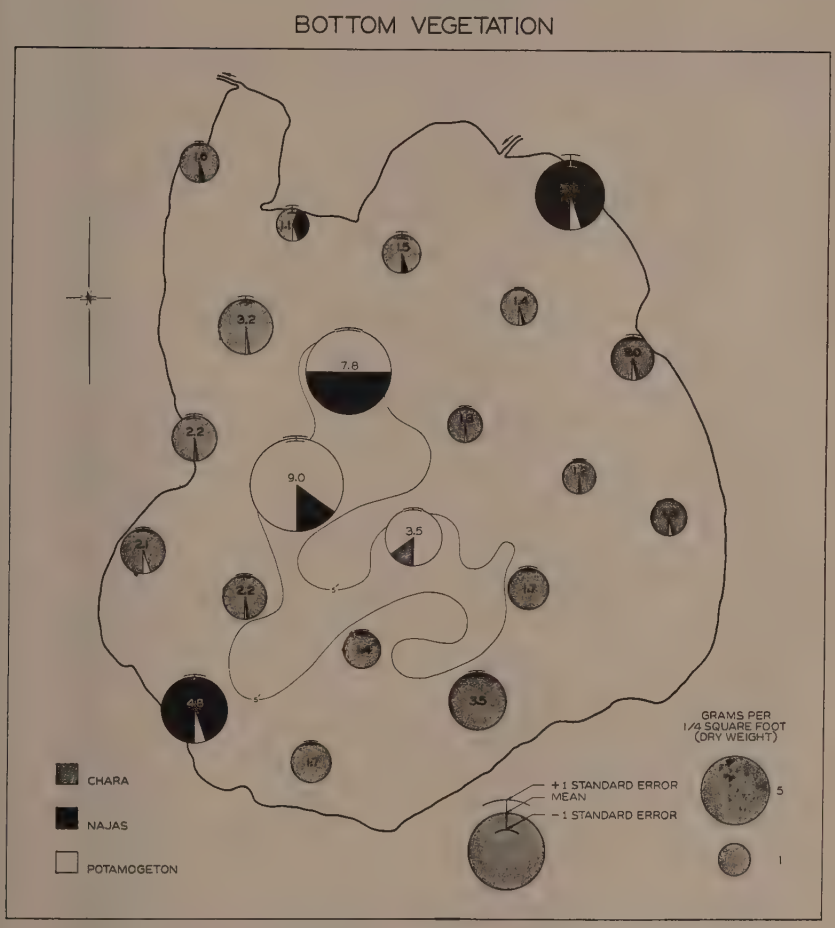


FIG. 2. Abundance and composition of submerged vegetation in samples taken at 21 stations in Sugarloaf Lake on November 22, 1955. Mean dry weight of plant samples collected at each station is proportional to radius of circle; standard error of the mean is represented by a line indicating increase or decrease in length of the radius.

Invertebrates

We identified thirty-two kinds of invertebrates from the benthos of Sugarloaf Lake. The mean number of individuals collected at each station is listed in Tables II and III. Plotting the occurrence of

TABLE II

Average Number of Invertebrates Per One Quarter Square Foot in the Chara-Tanytarsus Association in Sugarloaf Lake

[Four samples from each station; tr. = less than 0.5]

Organisms	Stations													
	A	B	2	4	5	6	7	8	10	11	14	17	19	21
Sphaerium sp.	...	...	...	...	...	tr.	...	...	...	tr.	tr.	...	...	...
Chaoborus punctipennis	3	7	1	tr.	1	...	tr.	6	2	3	1	1	...	...
Pentaneura flavescens	3	1	1	tr.	...	...	...	...	tr.	tr.	...	1	2	...
Pentaneura monilis	6	1	1	...	1	1	2	3	tr.	3	2	tr.	1	...
Procladius sp.	38	34	16	22	13	1	18	27	14	27	21	19	10	8
Clinotanypus sp.	4	4	1	...	1	1	1	...	1	1	...	3	1	7
Calopsectrini	19	10	1	3	3	3	10	8	2	18	2	4	8	5
Microtendipes pedellus	2	3	4	2	2	6	8	9	3	13	8	2	4	4
Polypedilum spp.	65	61	20	35	25	11	42	1	16	31	36	60	81	43
Tanytarsus jucundus	20	86	5	144	4	12	3	11	49	4	14	2	...	3
Stictochironomus sp.	3	2	...	...	1	1	1	...	1	2	...	...	1	1
Cryptochironomus digitatus	11	14	...	4	1	1	1	2	3	1	5	1	1	1
Pseudochironomus sp.	...	...	...	...	1	1	2	2	tr.	1	1	1	18	2
Glyptotendipes sp.	5	12	5	38	...	...	...	...	20	...	...	...	...	...
Tendipes (*Tendipes*) sp.	...	tr.	...	1	...	...	...	1	tr.	3	1	...	1	...
Tendipes nervosus	5	17	4	4	6	34	18	25	7	43	71	18	14	26
Tendipes tendipediformis	...	...	...	...	...	...	...	...	...	...	...	...	...	tr.
Heleidae	8	8	5	4	6	2	3	7	4	9	11	8	17	23
Psychomyiidae sp. A	13	11	8	15	25	9	17	14	14	9	30	39	27	32
Polycentropus interruptus	3	2	1	...	1	tr.	1	6	1	4	1	1	...	1
Leptoceridae	...	tr.	tr.	...	...	...	...	...	...	tr.	1	1	1	1
Coenagrionidae	...	...	tr.	...	2	...	2	...	tr.	2	3	1	1	4
Libellulidae	...	...	...	...	1	1	1	...	1	tr.	2	1	2	1
Hexagenia sp.	...	...	...	...	...	...	tr.	1	...	...	...	...	tr.	1	1
Ephemerella sp.	...	...	...	...	...	tr.	...	...	...	...	1	...	...	...
Caenis sp.	57	10	1	4	1	25	14	14	1	38	43	5	30	16
Hydracarina	tr.	tr.	...	tr.	...	tr.	2	...	...	2	3	...	2	tr.
Orconectes sp.	...	...	tr.	...	tr.	tr.	...	...	...	tr.	tr.	tr.	...	1
Hyalella azteca	189	147	124	118	156	142	186	201	158	121	156	184	270	163
Hirudinea	...	...	1	...	...	...	1	1	tr.	tr.	3	tr.	1	1
Oligochaeta	...	...	tr.	tr.	1	1	...	...	1	2	...	...	1	...
Turbellaria	1	1	...	...	1	...	2	1	...	1	1	1	2	2

TABLE III

AVERAGE NUMBER OF INVERTEBRATES PER ONE QUARTER SQUARE FOOT IN THE CHARA-HEXAGENIA AND NAJAS-POTAMOGETON-(TENDIPES) ASSOCIATION IN SUGARLOAF LAKE

[Four samples from each station; tr. = less than 0.5]

Organisms	Stations									
	Chara-Hexagenia					Najas-Potamogeton -(Tendipes)				
	1	3	20	22	23	9	12	15	16	18
Sphaerium sp.	...	...	1	...	...	...	...	tr.	...	...
Chaoborus punctipennis	...	...	tr.	...	...	4	2	20	5	3
Pentaneura flavescens	tr.	tr.	1	tr.	1	2	1	5	8	2
Pentaneura monilis	1	2	1	...	1	3	2	3	6	2
Procladius sp.	9	9	14	4	20	12	15	3	3	9
Clinotanypus sp.	tr.	1	9	3	6	...	...	...	...	...
Calopsectrini	1	tr.	3	3	4	6	6	15	7	5
Microtendipes pedellus	5	3	1	tr.	tr.	4	12	12	14	8
Polypedilum sp.	25	4	36	9	84	5	115	6	...	34
Tanytarsus jucundus	14	1	3	1	2	...	...	...	2	...
Stictochironomus sp.	1	1	1	tr.	1	1	1	2	3	4
Cryptochironomus digitatus	1	1	1	...	1	tr.	...	tr.	1	....
Pseudochironomus sp.	...	...	6	13	16	1	...	1	1	1
Glyptotendipes sp.	2	...	tr.	...	...	...	...	...	...	..
Tendipes (*Tendipes*) sp.	...	...	1	...	1	8	13	45	27	1
Tendipes nervosus	1	1	3	1	4	30	11	32	24	7
Tendipes tendipediformis	...	...	...	...	...	tr.	6	2	16	...
Heleidae	2	3	16	2	16	2	2	4	5	8
Psychomyiidae sp. A	1	7	4	...	2	...	tr.	3	18	2
Polycentropus interruptus	1	tr.	...	...	1	...	4	3	2	tr.
Leptoceridae	...	...	1	1	1	tr.	13	1	1	3
Coenagrionidae	tr.	...	4	tr.	1	2	tr.	tr.	1	5
Libellulidae	tr.	...	2	1	1	2	1	3	3	1
Hexagenia sp.	1	1	3	8	15	...	...	...	...	...
Ephemerella sp.	...	...	...	...	...	...	...	...	1	...
Caenis sp.	...	1	139	3	48	7	111	21	21	42
Hydracarina	...	...	tr.	...	1	1	2	2	1	1
Orconectes sp.	...	...	...	...	...	...	tr.	...	...	...
Hyalella azteca	84	123	174	77	112	8	31	24	30	66
Hirudinea	...	...	1	...	1	...	1	3	2	7
Oligochaeta	2	...	...	2	...	3	tr.	...	...	3
Turbellaria	...	tr.	1	1	...	1	...	...	...	...

FIG. 3. Distribution and abundance of *Hyalella azteca* at 25 stations in Sugarloaf Lake on November 22–25. Mean number of animals per sample is given by a number in or beside each circle and is proportional to its radius; standard error of the mean is represented by a line indicating an increase or decrease in length of the radius.

FIG. 4. Distribution and abundance of *Chaoborus punctipennis* at 25 stations in Sugarloaf Lake. (For explanation see Fig. 3.)

invertebrate species on a map of the lake revealed several distributional patterns. Some animals were generally distributed; others were restricted to definite areas. Some species, although found throughout the lake, reached their highest concentration at specific

groups of stations. The most distinctive distributional patterns were of the following species:

Hyalella azteca. *Hyalella* exceeded all benthic animals in both density and frequency of occurrence; this amphipod seemed truly

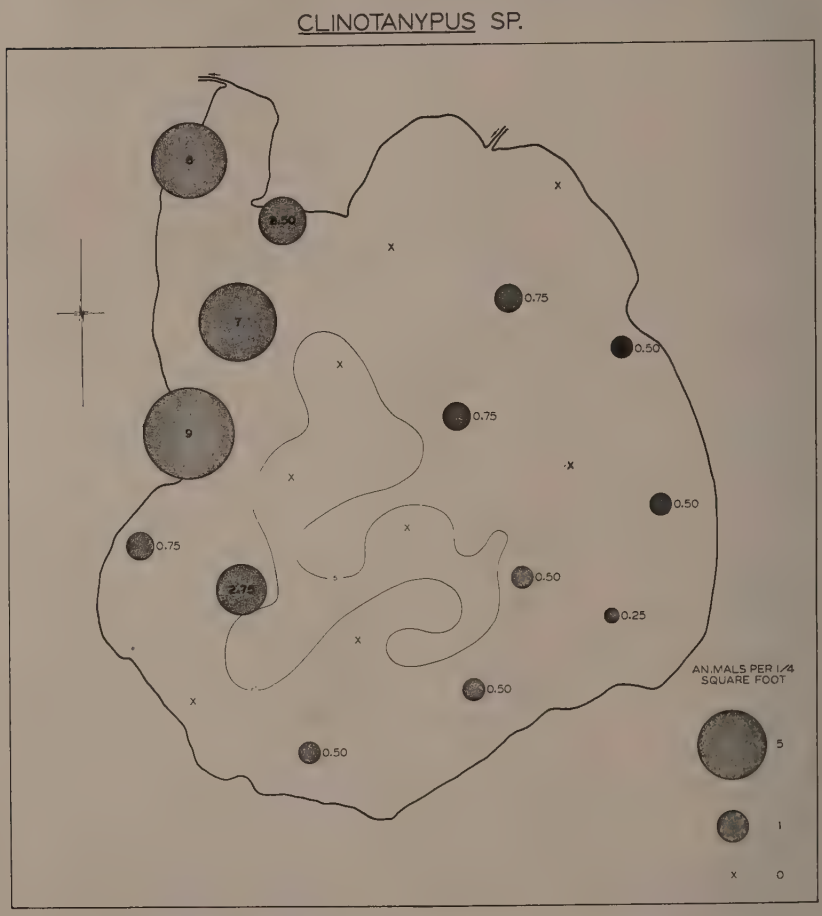


Fig. 5. Distribution and abundance of *Clinotanypus* sp. at 25 stations in Sugarloaf Lake. (For explanation see Fig. 3.)

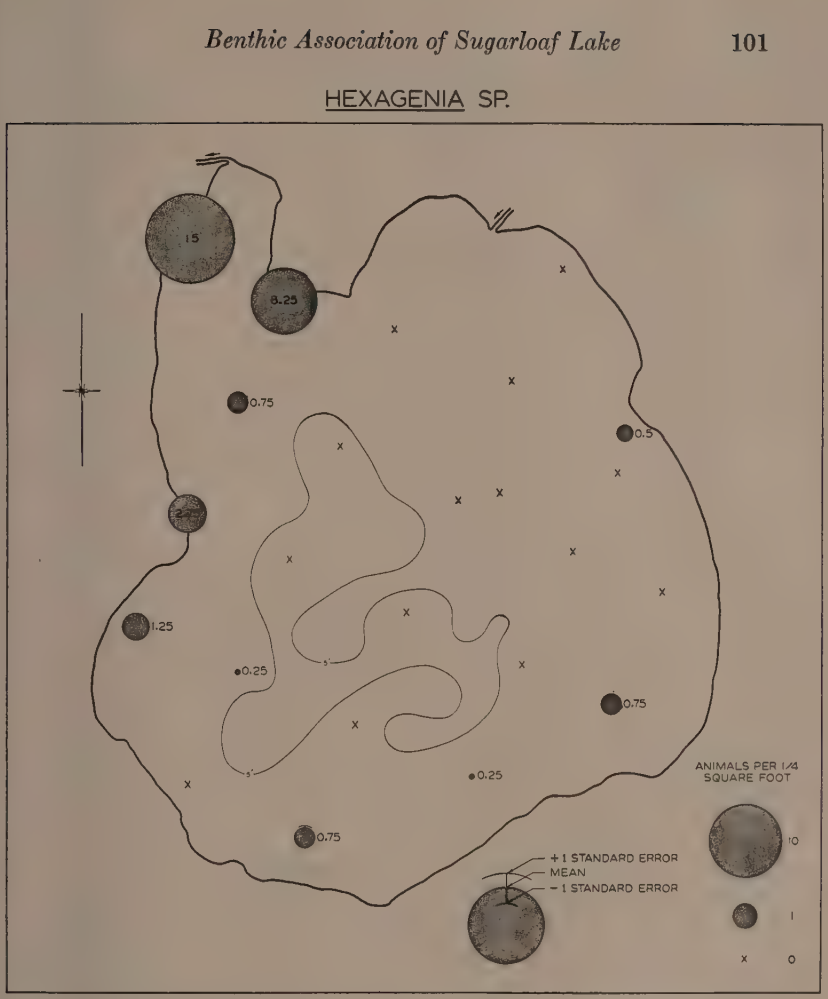


FIG. 6. Distribution and abundance of *Hexagenia* sp. at 25 stations in Sugarloaf Lake. (For explanation see Fig. 3.)

ubiquitous (Fig. 3). We found it in large numbers at all stations, but in lesser concentrations in the central depression.

Chaoborus punctipennis and *Tendipes* (subgenus *Tendipes*) spp. We found large numbers of these two insects below the five-foot con-

tour (Fig. 4). Even higher concentrations occurred in the sublittoral zone (Anderson and Hooper, 1956). A few individuals also appeared throughout the shallower areas.

Clinotanypus sp. This species occurred in greatest numbers at

FIG. 7. Distribution and abundance of *Tanytarsus jucundus* at 25 stations in Sugarloaf Lake. (For explanation see Fig. 3.)

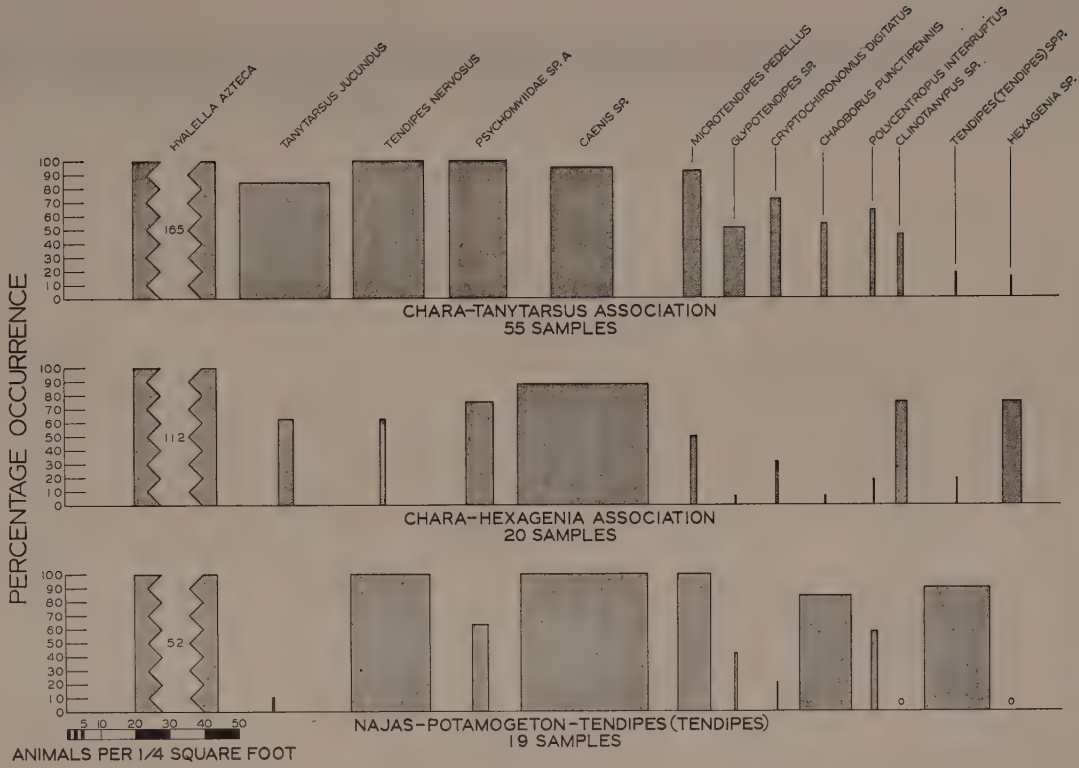


FIG. 8. Benthic associations of the littoral zone of Sugarloaf Lake. Frequency and density of twelve of the more abundant invertebrates are shown for each association.

stations along the windward shore (Fig. 5). Other areas had few *Clinotanypus*; we found none in the central depression.

Hexagenia sp. We found nymphs of this mayfly only in the firm substrate of the shallower on-shore stations around the periphery of the basin (Fig. 6).

Tanytarsus jucundus and *Glyptotendipes* sp. These midges were concentrated in the central portion of the lake basin (Fig. 7). Nothing in the soil or vegetation analyses, or in the physical configuration of the basin distinguished the area of concentration from the surrounding lake bottom. In the absence of evidence that either the soil or the vegetation was distinctive, we can only suggest that wind or water currents may have concentrated eggs or early larval stages of these two species in this part of the basin.

Biotic Associations

The variety of habitats encountered at the 24 stations is small compared to that in lakes having complex basins, irregular shore lines, and extensive shoals (Eggleton, 1952). Soil and vegetation analyses indicated that the littoral zone was remarkably uniform. The regularity of the shore line and of the lake basin tended to create such uniformity.

Principal variations encountered in the lake bottom were increases in firmness and in ash content of sediments with increasing exposure to wave action. The more compact bottom occurred at depths of two feet or less in the sheltered bays, but extended into the lake to depths of three to four feet along the west and southwest shores, where wave action was most severe.

Qualitatively, the animal assemblage of the shallow zone resembled that of the deeper water. A few forms, such as the burrowing mayfly *Hexagenia* sp., seemed almost restricted to this zone. Another mayfly, *Caenis* sp., reached its highest concentration here. The majority of species found here, however, were more abundant in other parts of the lake. This assemblage has been termed the *Chara-Hexagenia* association.

At slightly greater depths and in more protected areas, where the bottom was less compact, *Chara* remained the dominant plant, but the animal assemblage differed considerably. Two species of midges (*Tanytarsus jucundus* and *Cryptochironomus digitatus*) and one caddis fly (*Psychomyiidae* sp. A) were most abundant here, although they

occurred also in other areas (Tables II and III). This zone, termed the *Chara-Tanytarsus* association, constituted over half of the lake basin.

In the more protected parts of the littoral zone, *Chara* was replaced by *Najas* and *Potamogeton* as the predominant vegetation. This replacement occurred in the central depression below the five-foot contour, and at depths of three to four feet in the protected bays at the north and south ends of the lake. Although this zone was not well differentiated from the *Chara-Tanytarsus* association in bottom type, it was marked by greater standing crops of rooted aquatic vegetation. (*Tendipes*) sp. and *Chaoborus punctipennis* were characteristic of this zone.

The differences between the three biotic associations described above were chiefly quantitative. To illustrate these differences, we made frequency-density diagrams of 12 more abundant invertebrates (Fig. 8). All forms diagramed, we believe, were represented in the data by a single species. The dimensions of the rectangle representing each species indicate its average abundance and its frequency in all collections from each association. This diagram emphasizes that each association consists of a mixture of distinctive and ubiquitous species, and that differences in animal assemblages appear only when quantitative data are compared for a large number of forms.

Summary

1. We collected samples of bottom fauna, submerged plants, and bottom soil at 22 stations within the littoral zone of a shallow eutrophic lake.

2. Soil samples were quite uniform in texture and chemical composition. The principal variation was a higher ash content and a slight decrease in organic matter of the shallow-water sediments and the sediments of exposed shores.

3. *Chara* was the predominant submerged plant except in the central depression and in the more protected bays. Here *Najas* and *Potamogeton* were more important.

4. Certain species appeared to be associated with depth and soil conditions; other forms appeared to be distributed rather uniformly. Two midges, *Tanytarsus jucundus* and *Glyptotendipes*, were concentrated in a small area that could not be distinguished from the rest of the basin by depth, soil, or vegetation type.

5. We have described three biotic associations for the littoral zone. These associations are distinguished on the basis of soil and vegetation characteristics and quantitative differences in animal assemblages.

LITERATURE CITED

Anderson, Richard O., and Frank F. Hooper. 1956. Seasonal Abundance and Production of Littoral Bottom Fauna in a Southern Michigan Lake. Am. Micros. Soc., Trans., 75: 259–270.

Andrews, Jay D., and Arthur D. Hasler. 1944. Fluctuations in the Animal Populations of the Littoral Zone in Lake Mendota. Wis. Acad. Sci., Arts, and Letters, Trans., 35: 175–185.

Ball, Robert C. 1948. Relationship between Available Fish Food, Feeding Habits of Fish and Total Fish Production in a Michigan Lake. Mich. State College Agric. Exp. Sta., Tech. Bull., No. 206. 1–59.

Brundin, Lars. 1949. Chironomiden und andere Bodentiere der Sudschwedischen Urgebirgsseen. Inst. Freshwater Res., Fishery Board of Sweden, Report No. 30. 1–913.

Cooper, Gerald P. 1953. Population Estimates of Fish in Sugarloaf Lake, Washtenaw County, Michigan, and Their Exploitation by Anglers. Pap. Mich. Acad. Sci., Arts, and Letters, 38: 163–186.

Eggleton, Frank E. 1931. A Limnological Study of the Profundal Bottom Fauna of Certain Fresh-Water Lakes. Ecol. Mono., 1: 231–331.

—— 1952. Dynamics of Interdepression Benthic Communities. Am. Micros. Soc., Trans., 71: 189–228.

Hooper, Frank F. 1956. Some Chemical and Morphometric Characteristics of Southern Michigan Lakes. Pap. Mich. Acad. Sci., Arts, and Letters, 41: 109–130.

Krecker, Frederick H., and L. Y. Lancaster. 1933. Bottom Shore Fauna of Western Lake Erie: A Population Study to a Depth of Six Feet. Ecology, 14: 79–93.

Moffett, James W. 1943. A Limnological Investigation of the Dynamics of a Sandy, Wave-Swept Shoal in Douglas Lake, Michigan. Am. Micros. Soc., Trans., 62: 1–23.

Neel, Joe Kendall. 1948. A Limnological Investigation of the Psammon in Douglas Lake, Michigan, with Especial Reference to Shoal and Shoreline Dynamics. Am. Micros. Soc., Trans., 67: 1–53.

Pennak, Robert W. 1940. Ecology of the Microscopic Metazoa Inhabiting the Sandy Beaches of Some Wisconsin Lakes. Ecol. Mono. 10: 537–615.

Papers of the Michigan Academy of Science, Arts, and Letters
Vol. XLIII, 1958 (1957 Meeting)

A PRELIMINARY STUDY OF THE NUTRITIONAL ECOLOGY AND FOOD HABITS OF THE CHUBS (LEUCICHTHYS SPP.) AND THEIR RELATION TO THE ECOLOGY OF LAKE MICHIGAN[1]

SILVESTRE V. BERSAMIN
University of Michigan

Introduction

The deepwater chubs (*Leucichthys* spp.) are presently of considerable importance in the commercial fisheries of Lake Michigan. The disappearance of the lake trout has reduced the dangers of natural predation to chubs, but man has increased his rate of harvesting them (Moffett, 1957). The chubs are now the mainstay of commercial fishing in the open lake.

This investigation aims to make a thorough analysis of the food habits of five of the seven chub species to define their position in the food chain of the lake. Other objectives are to determine the relation of the bathymetric distribution of the chubs to the vertical distribution of *Mysis* and *Pontoporeia*, the two crustaceans which constitute the principal items in their diet, as well as to correlate feeding with information on population levels and rates of growth.

Materials and Methods

The materials used in this study were collected in 1954 and 1955 from 15 stations around Lake Michigan by the United States Fish and Wildlife Service during the fishery and limnological cruises of the Service's research vessel "Cisco." The majority of the specimens were collected from six locations (Table I). Collections were made with gill nets set obliquely from surface to bottom (similar to those used by Fry, 1937) at about 25 fathoms and with trawl nets which collected along the bottom at various depths, at different times of the day and night. The specimens were grouped in the following 2-inch length groups: 4 to 5.9, 6 to 7.9, 8 to 9.9, and 10 to 11.9 inches.

[1] Published with permission of the U.S. Fish and Wildlife Service, Ann Arbor, Michigan. Contribution from the Department of Fisheries, University of Michigan.

TABLE I

LAKE MICHIGAN FISHING STATIONS

Port	Depth in fathoms
A. West Shore	
Manistique	15–51
Sturgeon Bay	15–51
Manitowac	0–45
Sheboygan	18–48½
Port Washington	11–62
Racine	28–75
B. East Shore	
Charlevoix	16–50
Grand Traverse Bay	9–35
Frankfort*	0–39
Ludington	16–74
Grand Haven*	9–50
Holland	23½–27
South Haven	14–40½

* Home ports

The following species were represented: *Leucichthys hoyi*, *L. zenithicus*, *L. reighardi*, *L. alpenae*, and *L. kiyi*.

The contents of 2,437 stomachs from chubs caught during different seasons of the year have been subjected to the following analyses: (a) separation and identification of the various organisms; (b) determination by actual count of the number of each organism in each stomach; (c) measurement of the total volume of individual stomach contents (displacement method); (d) estimation of the relative degree of fullness of the organ; and (e) nutritional analysis of the principal food components.

RESULTS AND DISCUSSION

Of the stomachs opened 1,001 (41 per cent) contained identifiable organisms or remains, 805 (33 per cent) contained food too thoroughly digested to identify, and 632 (26 per cent) were empty. *Pontoporeia hoyi* Smith was the predominant organism in the stomachs, with 60 per cent occurrence. *Mysis relicta* Lovén follows with 38.1 per cent of occurrence. Generally, either *Mysis* or *Pontoporeia* was found in stomachs, but, in some instances, both occurred in the same stomach.

An acanthocephalan parasite in different stages of larval develop-

TABLE II

SUMMARY

EXAMINATION OF STOMACH CONTENTS OF *LEUCICHTHYS* SPP.

(Percentages shown in parentheses)

Species	Number Examined	With Identifiable Organisms	Digestion thorough, Unidentifiable	Empty	Range in Depth (fathoms)	Range in Length inches)	Predominant Food Organism	Per Cent of Occurrence of *Pontoporeia*	Per Cent of Occurrence of *Mysis*	Per Cent of Occurrence of Species in Catch
L. hoyi	1,618 (66.4)	751 (46.5)	458 (28.3)	409 (25.3)	9–75	2.0–11.9	Pontoporeia	66.6	33.4	66.4
L. zenithicus	138 (5.7)	69 (50.0)	34 (24.6)	35 (25.3)	13½–41	6–11.9	Mysis	35.3	64.7	5.7
L. alpenae	27 (1.1)	20 (74.1)	4 (14.8)	3 (11.1)	9–50	6–11.9	Mysis	5.0	95.2	1.11
L. kiyi	16 (.66)	11 (68.8)	0 (0)	5 (31.2)	33–75	6–11.9	Pontoporeia	69.7	30.3	.66
L. reighardi	96 (3.94)	43 (44.7)	24 (25.0)	29 (30.3)	33–41	6–9.9	Pontoporeia	51.1	46.6	3.94
Unidentified	542 (22.3)	107 (19.7)	285 (53.2)	150 (27.6)	9–41	2.0–11.9	Pontoporeia	49.7	50.5	22.3
Totals:	2,437 (100.0)	1,001 (41.0)	805 (33.0)	631 (26.0)	9–75	2.0–11.9	Pontoporeia Mysis	5.0–69.7	30.3–95.2	

TABLE III

SUMMARY OF FOOD ITEMS FOUND IN THE STOMACHS OF CHUBS (*LEUCICHTHYS* SPP.) IN LAKE MICHIGAN

Organisms	Species Where Found	Date of Occurrence	Depths in Fathoms	Size of Fish in Inches	Degree of Digestion	Per Cent Occurrence
Crustacea: *Pontoporeia* (Larval and adult stages)	*L. hoyi* *L. reighardi* *L. kiyi* *L. alpenae* *L. zenithicus*	May June July Aug. Oct. Nov.	9–75	2.0–11.9	Slight to thorough	24.9
Mysis (Larval and adult stages)	*L. hoyi* *L. reighardi* *L. kiyi* *L. alpenae* *L. zenithicus*	May June July Aug. Sept. Oct. Nov.	9–75	4.0–11.9	Slight to thorough	17.1
Acanthocephala (Larval stages)	*L. hoyi* *L. reighardi* *L. kiyi* *L. alpenae* *L. zenithicus*	May June July Aug. Sept. Oct. Nov. Dec.	9–74	2.0–11.9	Very slight to unaffected	13.7

Insecta: (Larval and adult forms) Diptera Fam. Chironomidae Fam. Mycetophidae Coleoptera Fam. Elateridae Fam. Coraleidae Hemiptera Fam. Notonectidae Homoptera Fam. Cicadellidae	*L. hoyi* *L. reighardi* *L. kiyi*	May June July	15–51	4.0–11.9	Partial to thorough	1.18
Mollusca: (Juvenile and adult forms) *Valvata sincera* Sphaeriidae (fingernail clam) *Pisidium* *S. tenue*, Prime *S. corneum*, Linn *P. lilljeborji*, Clessin *P. conventus*, Clessin *P. casertanum*, Poli	*L. hoyi* *L. reighardi* *L. kiyi*	May June	9–60	6.0–9.9	Slight to almost halfway	.69
Chub's eggs (diff. developmental stages)	*L. hoyi* *L. reighardi* *L. kiyi* *L. zenithicus* *L. alpenae*	May June Oct. Nov.	9–74	4.0–11.9	Very slight	4.43
Miscellaneous: Mud and detritus, sand and bits of gravel, digested plant and animal matter	*L. hoyi* *L. reighardi* *L. kiyi* *L. zenithicus*	May June July Aug. Sept. Oct.	9–74	2.0–11.9	Halfway to thorough	2.09

ment was present in many of the stomachs. Small numbers of a variety of insects in their larval, pupal, and adult stages were also encountered, namely: Diptera-Phoridae, Chironomidae, Mycetophidae; Homoptera-Cicadellidae. Of the fresh-water mollusks, the fresh-water snail, *Valvata sincera* and the fingernail clams (Sphaeriidae) were occasionally found.

Another important constituent of food consists of fish eggs tentatively identified as those of chubs in various stages of development. These eggs were in the stomachs of chubs taken during the months of May, June, October, and November. Occasionally, particles of sand, mud, small bits of gravel, undigested plant remains, and empty capsules of eggs were encountered.

Pontoporeia had been eaten by chubs taken within the depth range of 9 to 70 fathoms. It was most abundant in stomachs of fish caught at about 14 to 23 fathoms. Few were encountered in collections from waters shallower than 9 and deeper than 41 fathoms, and they were rare in chubs taken at depths greater than 71 fathoms. *Mysis* occurred in greatest numbers in stomachs of chubs taken from 71 to 74 fathoms. At this depth individual *L. hoyi*, 6.0 to 7.9 inches long, were found to contain as many as 720 slightly digested *Mysis* (sometimes dominated by larval forms but with some adult stages). The depth distribution of chubs that had eaten *Mysis* was from 14 to 74 fathoms, but they were most common at depths of 25 to 49 fathoms.

Pontoporeia occurred more frequently in the food of chubs during June and July. *Mysis* occurred more frequently in July, when stomachs of *L. hoyi* contained the greatest numbers of adult and larval forms. *Mysis* continued abundant in stomachs collected during August. This period of dominance coincides with the period of greatest growth for at least two species of chubs. Allen (personal communication) in his studies on the biology of the chubs set June as the usual time of annulus formation for *L. reighardi*; July and August for *L. alpenae*.

Mysis and *Pontoporeia*, associated with the lake bottom, are mainly exploited by chubs, sculpins (Cottidae), and the burbot (*Lota*). The presence of *Pontoporeia* and *Mysis* in various developmental stages in the stomachs of chubs caught during the different seasons and depths indicate that the vertical distribution of these crustaceans may be related to the distribution of chubs. Beeton in

his present studies on the breeding habits of *Mysis* and *Pontoporeia* states (personal communication) that these organisms start their reproductive activities in November and last till spring. Little reproduction is done in summer and none has been observed in September and October.

The invertebrates seem to thrive fairly well and maintain their prolificity under bottom environmental conditions. An abundance of food should be ever present from the earlier and critical stages of the chubs' development up through their remaining existence if they are to provide adequate commercial fishing.

Mysis relicta Lovén, a large if not the largest and most common crustacean in the habitat, is one of the best sources of fish food. To supplement their diets, the chubs eat various available aquatic and terrestrial insects in various developmental forms. Occasional larval forms of mollusks, plant matter, and organic detritus are also taken. The fingernail clam has a peculiar habit of inhabiting great depths of the lake where no other mollusks could normally thrive.

L. alpenae: The specimens were caught at depths ranging from 9 to 50 fathoms of water. The predominant food was *Mysis*, which was eaten both in adult and larval forms. *Mysis* constituted 95.2 per cent, whereas *Pontoporeia* formed only 5 per cent of the total food taken. The size of the fish ranged from 6 to 11.9 inches. The biggest contained about 458 slightly digested *Mysis* in adult and larval forms. *L. alpenae* constituted 1.11 per cent of the total catch.

L. kiyi: These groups of fish were caught at depths ranging from 33 to 75 fathoms. Hile and Deason (1944) state that the *kiyi* has the deepest habitat among the Michigan chubs. The predominant food consisted of *Mysis*, which was found mostly in adult form. Large concentrations of *Mysis* occur within the habitat of the *kiyi*, who feed directly on them. Their abundance and availability at these depths explain why the *kiyi* are seldom found above 33 fathoms of water. Other reasons are probably due to preference to cold water, strong pressures, darkness, and avoidance of strong currents (Hile and Deason, 1944). Size of fish ranged from 6 to 11.9 inches. *Pontoporeia* formed 69.7 per cent of its food and *Mysis* constituted 30.3 per cent. The former were found from 33 to 41 fathoms and the latter occurred from 44 to 75 fathoms. A specimen 8.0 to 9.9 inches long contained as many as 202 slightly digested *Mysis*. The *kiyi* is the least scarce among the chubs. It constituted only .66 per

cent of the total catch. Two fish were found to contain eggs of their own kind.

L. reighardi were concentrated at depths of 33 to 41 fathoms in May 10, 1954, with adult *Pontoporeia* constituting 51.1 per cent of the total food content and *Mysis* occupying only 46.6 per cent. The sizes vary from 6.0 to 9.9 inches. On May 8, they became most abundant at the 50-fathom mark. Thirteen fishes contained eggs of their own kind. They constituted 3.94 per cent of the entire catch for the period of investigation.

Cannibalism on their own eggs seems common in chubs. It may be explained by the availability and extreme abundance of eggs in the locality where the species both spawn and spend the greatest period of their existence. This serves as a source of concentrated nutriment for growth and a natural method of thinning population. Koelz (1929) gives the following spawning periods of the ciscoes: *L. artedi*—November to early December, in basins or shoal forms; *L. kiyi*—October, at great depths; *L. hoyi*—March, within 20 to 30 fathoms; *L. reighardi*—May, in shallower waters; *L. zenithicus*—November, in deeper waters; and *L. alpenae*—November, in deeper waters. This indicates the availability of eggs in almost all seasons of the year except from July to September. To these must be added the eggs and fry of the deep-water sculpins.

This study reveals a constant availability of the crustaceans *Mysis* and *Pontoporeia*, which constitute the main items in the diet of chubs. It is assumed that vertical movements of these two food constituents directly influence the vertical distribution of the chubs in their adult and even the fry stage, together with other organisms which directly feed on them. High selectivity in food habits seems unlikely, although chubs consume these two organisms more than others, as they abound in the areas and depths natural to the chubs.

Other foods may be taken incidentally, such as tiny snails, clams, aquatic insects, plants, and even their own eggs. The presence of insect larvae, pupa, and adult stages of aquatic insects suggests that occasionally chubs go to the surface to feed on insects, or that the latter may sink or be carried down to the bottom by currents. The chubs go in schools during spawning. This is illustrated by the fact that stomachs of the same sample group show close uniformity in contents as regards quality of organisms and other items and differ little in the degree of digestion and the general condition of the

stomach. In considering the large percentage of stomachs studied containing materials too thoroughly digested for identification, the differential digestibility of the food items found in the chubs under study provides indication of highly active feeding habits, especially before spawning, of rapid assimilation of food materials and incorporation into fish flesh, and of an equally high speed of replacement of food.

It has been observed that the stomachs of bigger fish usually contain the bigger adult crustaceans in greater numbers. Among the smaller fish the stomachs are generally empty; often the contents may be thoroughly digested due to a more rapid rate of digestion or inability to capture food within short periods. Deason and Hile (1944) state that growth for smaller young coregonids is more rapid in later years than in the larger fish.

A large percentage of the stomachs opened contained thoroughly digested materials presumably composed of plant and animal matter. Insect larvae play an important role as food of the fish so a knowledge of their distribution and abundance would aid in the management of the fishery.

It is assumed that the thorn-headed worm (Acanthocephala), commonly found in a great majority of the samples examined acts as intermediate host of this parasite. Woodhead (personal communication) states that in the life cycle of the Acanthocephalan parasite, the eggs are eaten by the chubs (intermediate host), where they develop into the larval forms and various immature stages of development. The completion of the life cycle requires that the larval host (the chub) be eaten by the final host of the adult worm, which is usually a much larger fish—the trout, burbot, or larger ciscoes—where they develop to sexual maturity. The parasite eggs are laid with the feces of the fish and settle at the bottom. No sexually mature Acanthocephalan worm was found in any of the stomachs opened, which establishes the chub as the secondary host.

Newly hatched chubs also consume an abundance of these crustaceans (*Bull., Buff. Soc. Nat. Sci.*, Vol. XIV, No. 3). This peculiar use of crustaceans in the diet is retained throughout their life. The crustaceans feed on microscopic plants like algae and diatoms, which synthesize their own food from soluble inorganic substances and gases in the water. Small crustaceans are also eaten by bigger forms which, in turn, constitute part of the diet of the chubs. This con-

stitutes the food cycle in the lake. Successful conservation and management of the lake fisheries depend on the maintenance of this cycle. Failure of a single factor in the chain has disastrous effects on fish populations. This cycle of interdependence places the crustacean group in a highly important category in the food chain from the point of view of chub fishery economy.

Besides an extensive lamprey control program, adequate measures should be taken for the proper utilization and conservation of the invertebrate population of the lake to benefit the chub fishery. Records show that the present abundance of crustaceans is more than enough to supply adequate food to the fish population of the lake and even to the rapidly increasing bloater. A natural resource could be exhausted so it becomes essential to strengthen the crustacean category as well as those below it in the food chain. An increase in the microscopic plankton, such as algae and diatoms, which constitute the bulk of crustacean food, should be considered. If this supply gets below the limit for the normal operation of the food chain endangering the invertebrate category, then lake fertilization should be resorted to in an effort to increase the planktonic population.

Cruise reports of the United States Fish and Wildlife Service, 1957,[2] state that chubs of the same length weigh more than they did in 1930, indicating that probably there is a greater supply of food per pound of fish. Vinogradov (1953), in his nutritive analysis of these crustacean components, reveals that the chubs are being provided with adequate nutritive requirements for normal growth.

Allen (1957) in his investigations on the biology of the chubs in Lake Michigan found age group III to be dominant for *L. alpenae* today. In 1923 it was age group IV and in 1928 age group III. For *L. hoyi* the dominant age groups for the earlier period were IV and V and have now dropped to III as should be expected because of its great increase (Cruise Reports, United States Fish and Wildlife Service, 1954–1955).

Before its disappearance from Lake Michigan, the lake trout and the burbot were given the distinction of occupying the top of a food chain consisting of smaller fishes such as chubs and sculpins, crustaceans, microplankton, algae, and diatoms. This food chain has now been altered with the appearance of the sea lamprey and the disap-

[2] U. S. Fish and Wildlife Service, M. V Cisco Cruise Reports, Ann Arbor, Michigan, 1954–1955.

pearance of the lake trout and burbot. In the event that all the bigger fish are eliminated the chub category becomes elevated in the chain.

The following is an illustration of the cycle of interdependence in the lake.

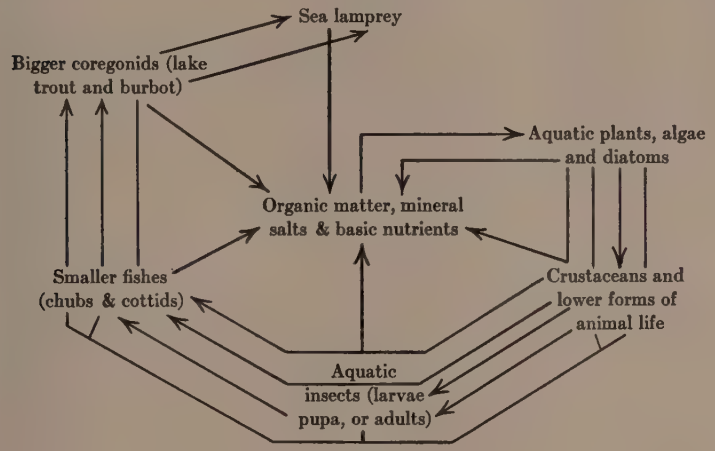

Sea lamprey
Bigger coregonids (lake trout and burbot)
Aquatic plants, algae and diatoms
Organic matter, mineral salts & basic nutrients
Smaller fishes (chubs & cottids)
Crustaceans and lower forms of animal life
Aquatic insects (larvae pupa, or adults)

FIG. 1

LITERATURE CITED

DEASON, HILARY J., AND RALPH HILE. 1947. Age and Growth of the Kiyi, *Leucichthys kiyi* Koelz, in Lake Michigan. Trans. Am. Fish. Soc., 74 (1944): 88–142.

ESCHMEYER, PAUL H., AND REEVE M. BAILEY. 1955. The Pigmy Whitefish, *Coregonus coulteri*, in Lake Superior. Trans. Am. Fish. Soc., 84 (1955): 162–199.

FRY, F. E. J. 1937. The Summer Migration of the Cisco, *Leucichthys artedi* (Le Seur), in Lake Nipissing, Ontario. Univ. Toronto Studies Biol., (44): 1–91, 27 text figs.

HILE, RALPH, AND HILARY J. DEASON. 1947. Distribution, Abundance, Spawning Season and Grounds of the Kiyi, *Leucichthys kiyi* Koelz in Lake Michigan. Trans. Am. Fish. Soc., 74 (1944): 143–165.

JOBES, FRANK W. 1949. The Age, Growth and Bathymetric Distribution of the Bloater, *Leucichthys hoyi* (Gill), in Lake Michigan. Papers Mich. Acad. Sci., Arts, and Letters, 33 (1947): 135–172.

—— 1943. The Age, Growth and Bathymetric Distribution of Reighard's Chub, *Leucichthys reighardi* Koelz in Lake Michigan. Trans. Am. Fish. Soc., 72 (1942): 108–135.

—— 1949. The Age, Growth and Distribution of the Longjaw Cisco, *Leucichthys alpenae* Koelz in Lake Michigan. Trans. Am. Fish. Soc., 76 (1946): 215–247.

KOELZ, WALTER. 1929. Coregonid Fishes of the Great Lakes. Bull. U. S. Bur. Fish., Part 2 (1927): 297–643.

LAGLER, KARL F. 1952. Freshwater Fishery Biology. 1st ed.; Dubuque, Ia.: Wm. C. Brown Company. 360 pp., 172 text figs.

LANGFORD, R. R. 1938. The Food of the Lake Nipissing Cisco, *Leucichthys artedi* (Le Seur), with Special Reference to the Utilization of the Limnetic Crustacea. Univ. Toronto Studies, Biol. Ser., 45: 143–190, 8 text figs.

MOFFETT, JAMES W. 1957. Recent Changes in the Deep-Water Fish Populations of Lake Michigan. Trans. Am. Fish. Soc., 86 (in press).

STONE, U. B. 1944. A Study of the Deep-Water Cisco Fishery of Lake Ontario with Particular Reference to the Bloater *Leucichthys hoyi* Gill. Trans. Amer. Fish. Soc., pp. 230–249.

VAN OOSTEN, JOHN. 1929. Life History of the Lake Herring, *Leucichthys artedi* Le Seur, of Lake Huron as Revealed by Its Scales, with a Critique of the Scale Method. Bull. U. S. Bur. Fish. (1928): 265–428.

—— 1937. The Age, Growth and Sex Ratio of the Lake Superior Longjaw, *Leucichthys zenithicus* (Jordan and Evermann). Papers Mich. Acad. Sci., Arts and Letters, 22 (1936): 691–711.

—— 1939. The Age, Growth, Sexual Maturity, and Sex Ratio of the Common Whitefish, *Coregonus clupeaformis* (Mitchell), of Lake Huron. Papers Mich. Acad. Sci., Arts, and Letters, Vol. 24, Part 2 (1938): 195–221.

VINOGRADOV, A. P. 1953. The Elementary Chemical Composition of Marine Organisms. Sears Foundation for Marine Research, Yale University. Memoir II, pp. 397–399.

WILSON, CHARLES B. 1928. The Macroplankton of Lake Erie. Bull., Buffalo Society of Natural Sciences, Vol. XIV, No. 3.

Papers of the Michigan Academy of Science, Arts, and Letters
Vol. XLIII, 1958 (1957 Meeting)

NOTES ON THE FEEDING PERIODICITY OF VARIOUS ORTHOPTERA

S. K. GANGWERE
Wayne State University, Detroit, Michigan

It is now accepted that Orthoptera are not continuously active night and day, although individuals of many species may be found moving around during both of these periods; that feeding is necessarily restricted to the hours of activity, which in most species number from ten to twelve or more; that feeding is discontinuous, seldom occupying an aggregate of more than one or two hours out of twenty-four. Nevertheless, several serious gaps remain in our knowledge. The present paper hopes to eliminate one of these gaps, namely, our imperfect understanding of the periodicity of feeding of nocturnal Orthoptera.

Larrimer and Ford (1922), Swenk and Wehr (1923), Shotwell (1930), and others have studied the diurnal feeding periodicity of various acridids or short-horned grasshoppers. They have shown that individuals of these different species begin feeding early (usually about 5:00 or 6:00 A. M.), often while still perched on the vegetation on which many spent the night. They continue feeding and begin working their way toward the ground as the air temperature rises. Peak feeding usually begins about 9:00 or 10:00 A. M. and continues at a gradually diminishing rate, satiation and the period of highest environmental temperatures coinciding to cut down feeding. With the late afternoon return of cooler, more favorable temperatures, together with renewed hunger, there may be a secondary, smaller peak of feeding, this occurring at the same time as the animals begin to reascend the vegetation (usually about 3:30 or 4:00 P. M.). This secondary peak of feeding ends abruptly at dusk. Parker (1924, 1930), Cowan and Shipman (1940), Shotwell (1941, 1942), and De Wet and Webb (1951) have demonstrated similar patterns of periodicity for the diurnal insects they investigated but were correct in emphasizing the influence of temperature rather than time of day in the control of feeding periodicity.

A few authors have made scattered, incomplete remarks about

the feeding periodicity of certain species of nocturnal Orthoptera; for example, Severin (1926) stated that the cricket *Acheta* feeds chiefly from 4:00 P. M. to 8:00 or 9:00 A. M. Such terse statements and the assumption that these insects have a feeding periodicity correlated with that of their movement and singing are all that is known about the matter, for nowhere is there a study dealing in any detail whatsoever with nocturnal periodicity patterns. This is to be expected, however, for most of these insects, unlike the diurnal acridids, are not economically important. Further, they present special problems in observation because they must be watched under artificial light.

Methods

I used several different approaches to the study of nocturnal feeding periodicity in the present investigation:

Baiting Exercises. The oatmeal trail method of collection, a technique developed by Hubbell (1956), I modified and used for the first time to study feeding periodicity. In this method the baiter walks along, allowing a fine trail of oatmeal flakes to fall upon the path, and later revisits the trail when the insects attracted to the bait are collected. In the experiments here reported the oatmeal trail was one-half mile long. It was laid early in the evening before dusk and was revisited at regular time intervals when numbers and species of individuals at the bait were recorded. I made no collections in order to avoid altering later counts. Readings of temperature and relative humidity were taken by means of Serdex instruments placed on the ground where the insects were feeding.

Observations upon Animals Caged in the Field. Twenty individuals of the katydid *Amblycorypha rotundifolia* were confined within a small open-floored screen cage (3′ x 3′ x 2′) placed in an oak-hickory woods, a normal habitat of this species, the cage including within its walls *Solidago caesia* and *Gaylussacia baccata*, both of which are favored food-plants. A second very large open-floored screen cage (4′ x 4′ x 6′) was placed in a marsh habitat, and in it were confined forty individuals of the katydid *Scudderia f. furcata* and thirty-five of *S. c. curvicauda*, both species commonly occurring in number in this habitat. This larger cage included within its walls a dense stand of characteristic marsh vegetation, including *Impatiens capensis*, *Polygonum sagittatum*, *Solidago canadensis*, and *Typha latifolia*,

all of which are favored food-plants. I visited both cages at intervals of one to three hours for five nights and several times during each day, observing movement, singing, and feeding, all of these being apparently unaltered by confinement.

Observations upon Uncaged Animals in the Field. During the course of field studies on the feeding behavior of Orthoptera, both nocturnal and diurnal, I tried to record the time of feeding as well as the weather conditions under which feeding occurred. Naturally, these data strongly reflect the frequency of observation, the information from two of the periods (4:00 to 8:00 P. M., 12:00 to 4:00 A. M.) being based upon fewer records than that from the other two periods. Nevertheless, I feel that these studies yield valuable and accurate information on feeding periodicity because they are based upon a very large number (153) of feeding records.

Results

Baiting Exercises. The data accumulated during the baiting studies are shown in Figs. 1–5, where the number of individuals found along the bait trail is plotted against the time of observation. Readings of temperature and humidity are recorded under each time interval. The camel cricket *Ceuthophilus meridionalis*, the cricket *Acheta assimilis*, and the roaches *Parcoblatta uhleriana* and *P. pensylvanica* were the only species of Orthoptera sufficiently abundant to be reported here.

Analysis of the data shows that in these geophilous, nocturnal insects feeding is negligible at dusk but accelerates with the approach of darkness. The peak of feeding occurs early in the evening (about 9:00 P. M.) and drops off abruptly by 11:00 or 12:00 P. M. Following this initial decrease there is a more gradual decrease in feeding until 4:00 A.M., when feeding becomes negligible. This general pattern of nocturnal feeding periodicity does not seem to be altered by changes in the climatic factors, although the latter are important in determining the relative amount of feeding at a given time.

The pattern of periodicity demonstrated by *Ceuthophilus* is characterized by a marked, early feeding peak and abrupt decline, not leveling off until early morning, whereas the two species of *Parcoblatta* have a gentler decline from the feeding peak. *Parcoblatta uhleriana* differs from *P. pensylvanica* in that the former is always found in greater numbers at the bait. This disparity is due either to differ-

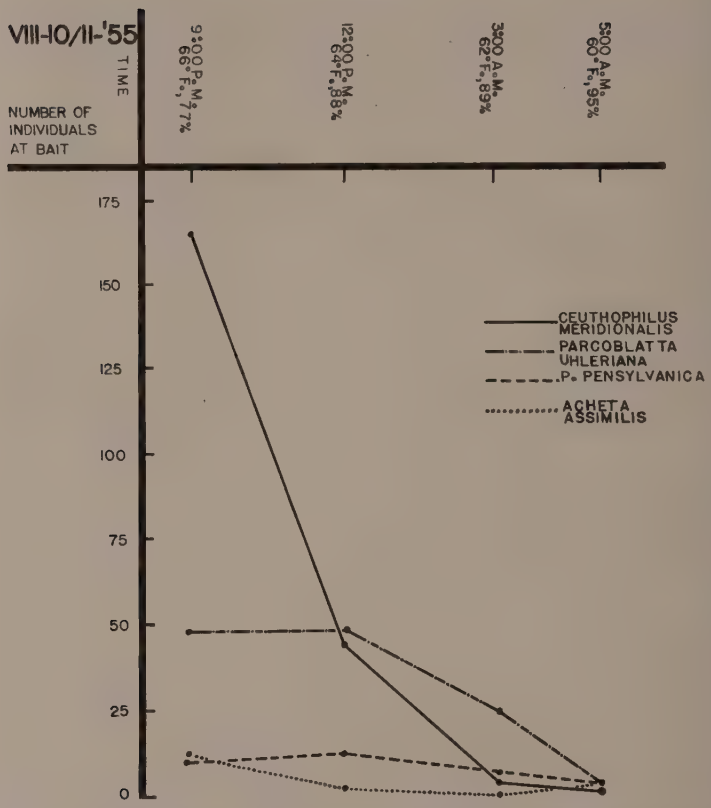


FIG. 1. Feeding periodicity of certain nocturnal Orthoptera based upon oatmeal baiting.

ences in population size or to differences in habits. *Acheta* is much more diurnal than the other species found at the oatmeal trail. I saw individuals of *Acheta* attracted to bait and heard them singing during all hours of both night and day, this tendency toward diurnal behavior being most pronounced on dark, cool summer days. Severin (1926) reported that *Acheta* feeds from 4:00 P. M. to 8:00 or 9:00 A. M. All field data available suggest that feeding of *Acheta* begins in the late afternoon, gradually building up to a peak about 8:00 P. M.,

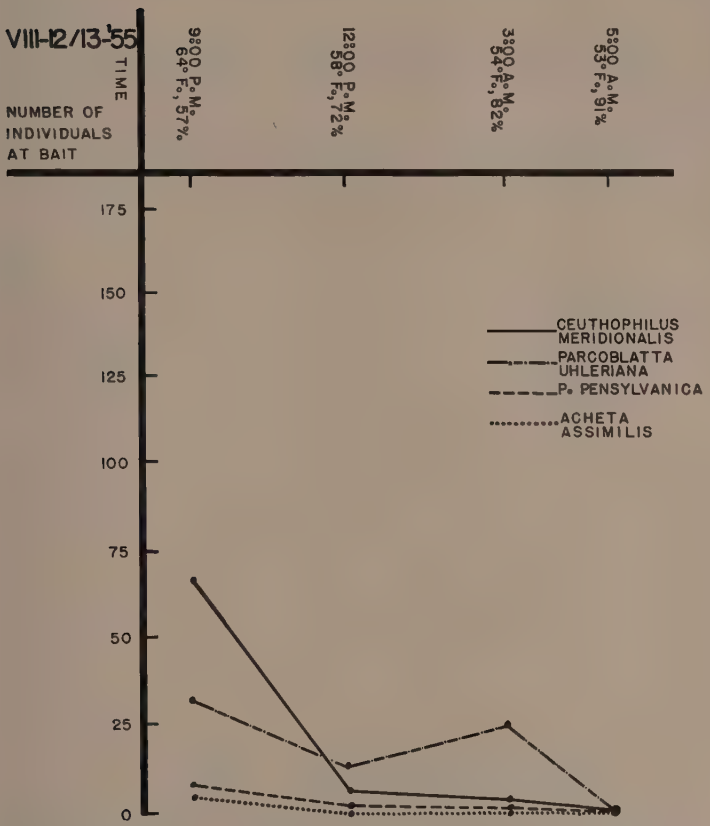


FIG. 2. Feeding periodicity of certain nocturnal Orthoptera based upon oatmeal baiting

dropping off after 9:00 P. M., gradually decreasing until almost negligible at 2:00 or 3:00 A. M., perhaps increasing temporarily early in the morning (6:00 to 7:00 A. M.) before virtually ceasing for the day at 8:00 to 9:00 A. M.

Observations upon Animals Caged in the Field. From 2:00 A. M. to 7:00 P. M., the individuals of *Amblycorpha rotundifolia* remained hidden and virtually motionless in the vegetation covering the forest floor. They moved over the vegetation, and the males sang from

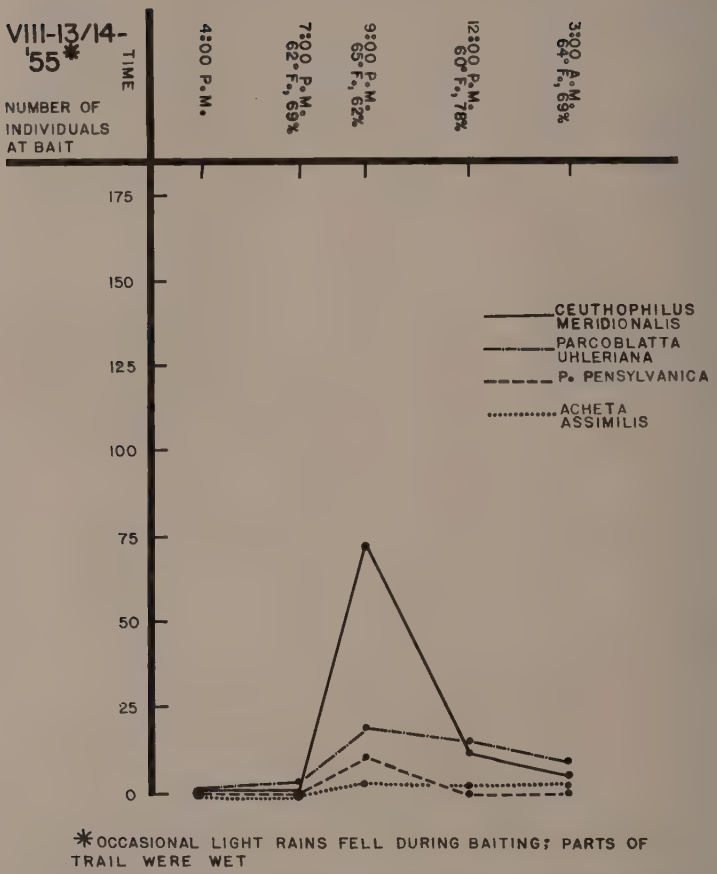


Fig. 3. Feeding periodicity of certain nocturnal Orthoptera based upon oatmeal baiting.

8:00 to 12:00 P. M., the period of maximum activity occurring from 9:00 to 11:00 P. M. Movement and singing diminished during the period from 12:00 to 2:00 A. M. Feeding was at a maximum early in the period of greatest activity and occurred sporadically at all other times of activity. Rainfall and low temperatures markedly reduced the insects' activity. *Scudderia f. furcata* and *S. c. curvi-*

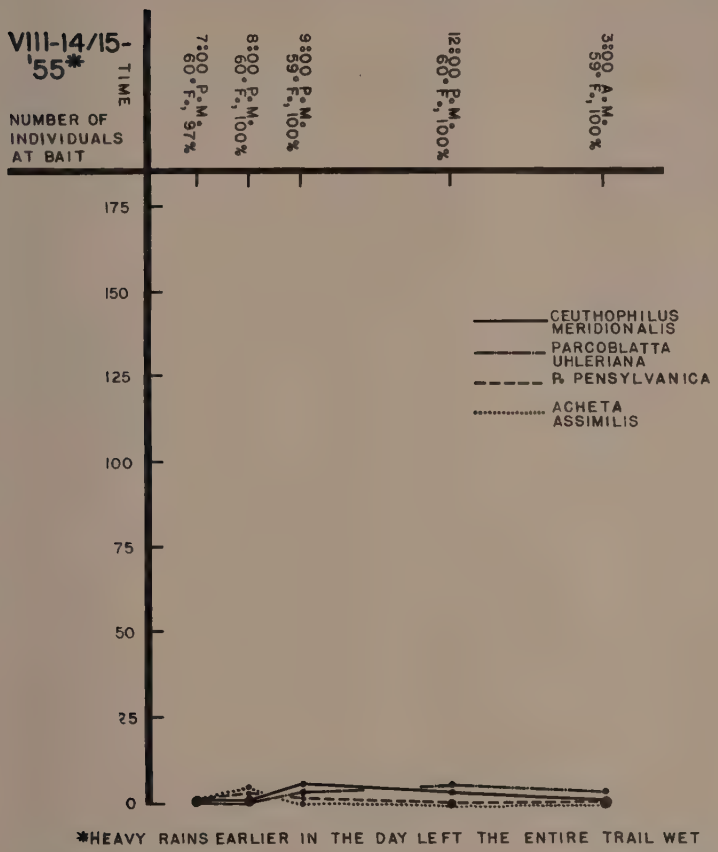


FIG. 4. Feeding periodicity of certain nocturnal Orthoptera based upon oatmeal baiting.

cauda, like *Amblycorypha rotundifolia*, are nocturnal, but they are incompletely so, for individuals of these two species sometimes walk, fly, and even feed diurnally, particularly in the late afternoon of cloudy, dark days. Feeding of *Scudderia* was at a maximum from 8:00 to 10:30 P. M., fairly heavy from 10:30 to 12:00 P. M., light from 12:00 to 2:00 A. M. and 4:00 to 7:00 P. M., being negligible at all other times. The periodicity patterns of the two species of *Scudderia* proved indistinguishable.

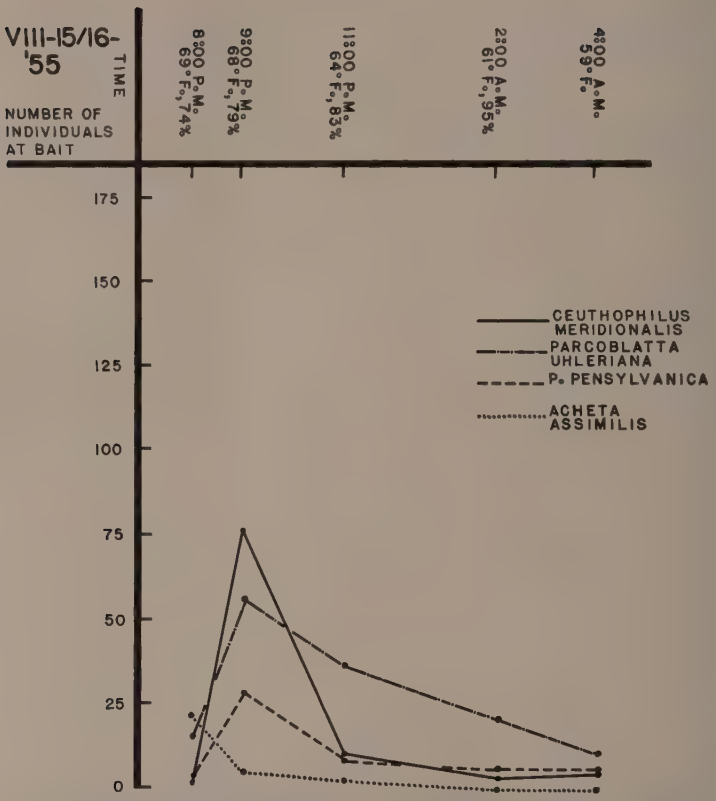


FIG. 5. Feeding periodicity of certain nocturnal Orthoptera based upon oatmeal baiting.

Observations upon Uncaged Animals in the Field. Data from feeding records of uncaged Orthoptera, both nocturnal and diurnal, have been worked into incomplete but informative graphs of feeding periodicity. On these (Figs. 6–8), the position of the bars shows the periods during which feeding occurred in each species. The relative width of each bar shows the percentage of feeding records of a species occurring in a given period. Gaps in the data are indicated by question marks.

These data show that, of the groups of Michigan Orthoptera

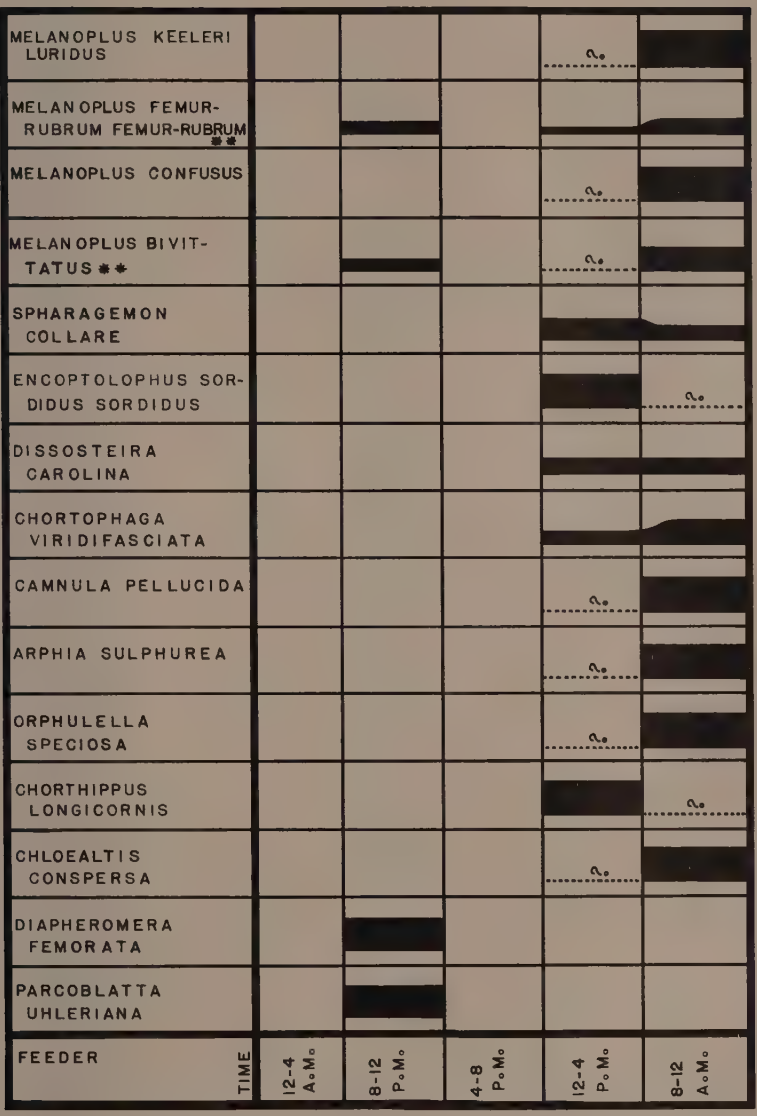


FIG. 6. Feeding periodicity of various Orthoptera based upon observations of feeding individuals in the natural habitats.

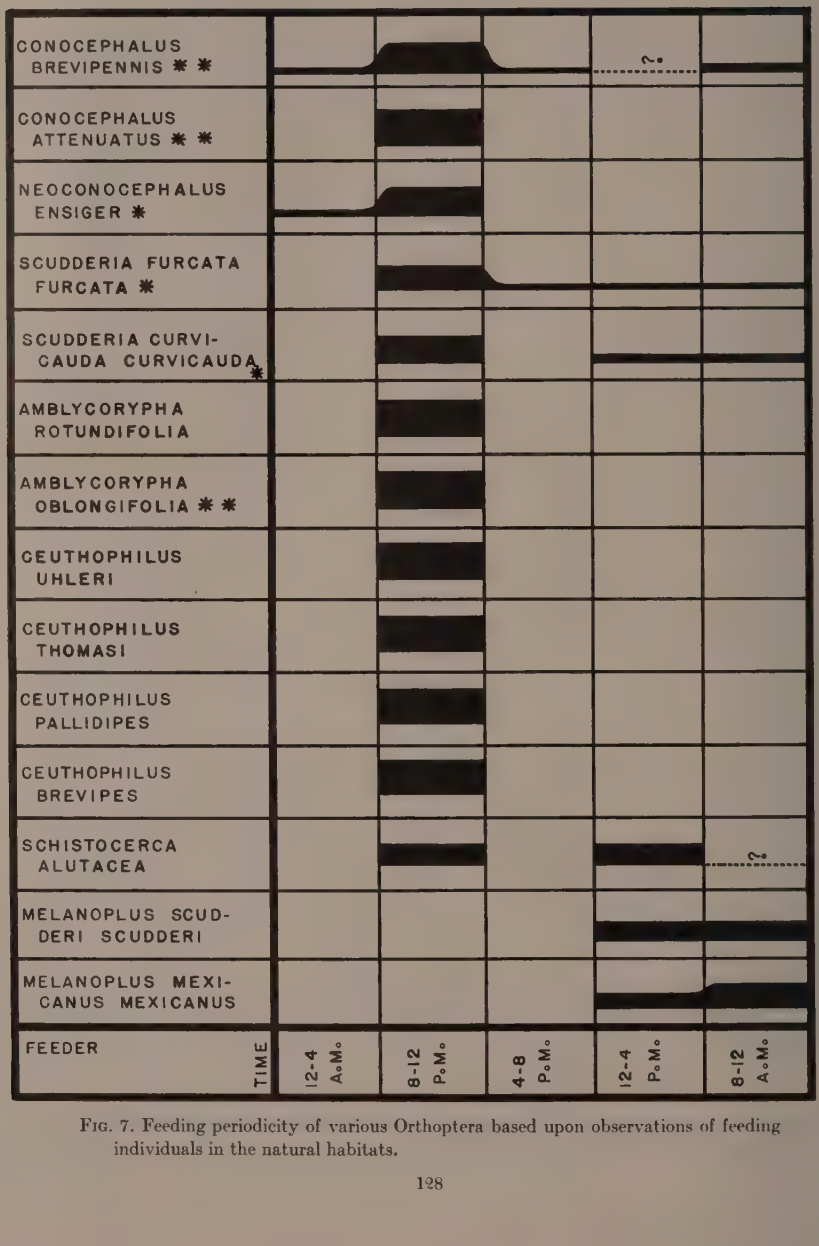


FIG. 7. Feeding periodicity of various Orthoptera based upon observations of feeding individuals in the natural habitats.

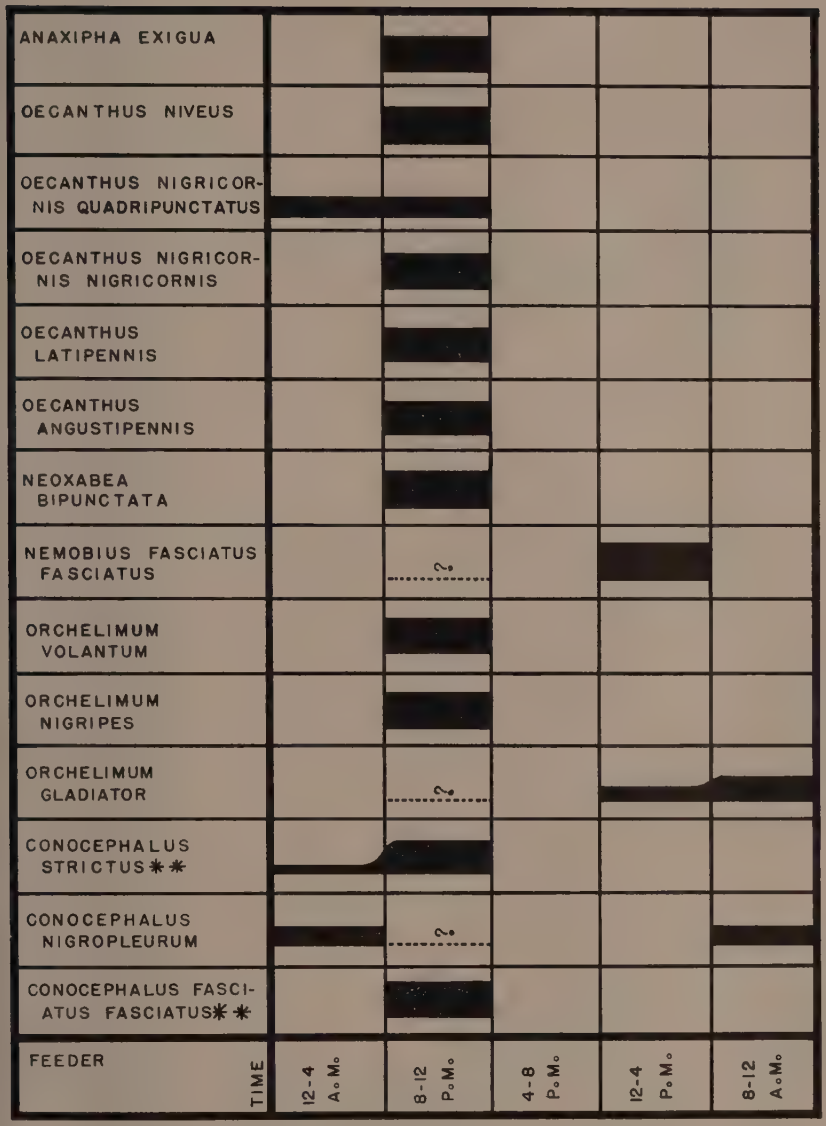


FIG. 8. Feeding periodicity of various Orthoptera based upon observations of feeding individuals in the natural habitats.

studied, most tend toward nocturnal feedings. Only one group, the Acrididae (*Chloealtis* to *Schistocerca* on Figs. 6 and 7) is composed of species which are characteristically diurnal in their feeding, but even here certain spine-breasts which inhabit marshes (*Melanoplus bivattatus*, *M. f.-r. femur-rubrum*) frequently feed at night. The remainder of the groups are composed of species with nocturnal feeding habits. This sweeping generalization must, however, be qualified with respect to the walking stick *Diapheromera*, the katydids *Scudderia*, *Conocephalus*, and *Orchelimum*, and the crickets *Acheta* and *Nemobius*.

Diapheromera femorata, when caged, fed both diurnally and nocturnally. Nevertheless, in its natural habitat it was most active at night, and it was never seen to feed during the day. The incompletely nocturnal pattern of *Scudderia* has already been discussed. With respect to the Conocephalinae, Cantrall (1943), in his excellent treatment of the ecology of the George Reserve orthopterans, calls this group primarily diurnal, stating that feeding, mating, and singing are mostly daytime activities. The present observations do not support such an idea of feeding, for the great majority of feeding records of the several species of *Conocephalus* and *Orchelimum* were made between 8:00 and 12:00 P. M., only a few being made during the daytime. *Orchelimum gladiator* was the lone exception. *Nemobius f. fasciatus*, like *Acheta assimilis*, is frequently found moving around during the hot part of the day although usually in a sheltered situation, and the single feeding record obtained for it was made during the afternoon. Notwithstanding this tendency toward diurnal activity, more extensive data should show that *Nemobius*, too, is incompletely nocturnal.

Summary and Conclusions

There are three patterns of feeding periodicity in the Orthoptera: diurnal, incompletely nocturnal,[1] and nocturnal. The incompletely nocturnal pattern is essentially a nocturnal one with some feeding during the day, especially under cloudy, dark conditions. The nocturnal pattern, characteristic of most groups of the Orthoptera, is not unlike the comparatively well-known diurnal, differing chiefly in time of feeding. Like the diurnal Orthoptera, nocturnal species

[1] The term *crepuscular* has been used in this sense, but it should be restricted to those patterns in which the greatest, if not all, activity is at dusk.

begin feeding when the conditions of light, temperature, and humidity allow them to resume activity after a period of quiescence. Once under optimum environmental conditions they begin peak feeding (about 9:00 P. M.). With satiety and changes in air temperature and humidity, feeding then begins to fall off, becoming negligible at about 4:00 A. M. The secondary peak of feeding seen in acridids does not materialize in nocturnal species because the level of temperature and humidity remains unfavorable until daylight, which in itself inhibits activity. Even though climatic factors are important in determining the relative amount of feeding at a given time they do not basically alter the periodicity pattern.

Acknowledgments

The author is deeply indebted to several persons whose assistance made possible the completion of this paper. Dr. T. H. Hubbell, of the University of Michigan Museum of Zoology, and Dr. I. J. Cantrall, of the same institution, have contributed numerous suggestions and were instrumental in giving the author access to the University's E. S. George Reserve, where much of the work was carried out. Professor Jessie Metcalf and Mr. Alfred Beeton, both of Wayne State University, and Dr. Cantrall rendered invaluable assistance by critically reviewing the manuscript.

LITERATURE CITED

Cantrall, I. J. 1943. The Ecology of the Orthoptera and Dermaptera of the George Reserve, Michigan. Univ. Mich. Mus. Zool. Misc. Publ., 54: 1–182.

Cowan, F. T., and H. J. Shipman. 1940. Control of the Mormon Cricket by the Use of Poisoned Bait. U. S. Dept. Agric. Circ., 575: 1–16.

De Wet, W. J., and D. Van V. Webb. 1951. Field Observations on the Behavior of Hoppers of the Brown Locust in the Swarming Phase. Union S. Africa Dept. Agric. Locust Res., Ser. 14, Sci. Bull., 337: 1–38.

Hubbell, T. H. 1956. A New Collecting Method: the Oatmeal Trail. Ent. News, 67: 49–51.

Larrimer, W. H., and A. L. Ford. 1922. The Daily Maximum Feeding Period of *Melanoplus femur-rubrum*. Can. Ent., 54: 141–143.

Parker, J. R. 1924. Observations on the Clear-winged Grasshopper (*Camnula pellucida* Scudder). Univ. Minnesota Agric. Exp. Sta. Bull., 214: 1–44.

Parker, J. R. 1930. Some Effects of Temperature and Moisture upon *Melanoplus mexicanus mexicanus* Saussure and *Camnula pellucida* Scudder. Montana Agric. Exp. Sta. Bull., 223: 1–132.

Severin, H. C. 1926. The Common Black Field Cricket *Gryllus assimilis* (Fab.) and Its Control. Journ. Econ. Ent., 19: 218–227.

Shotwell, R. L. 1930. A Study of the Lesser Migratory Grasshopper. U. S. Dept. Agric. Tech. Bull., 190: 1–34.

Shotwell, R. L. 1941. Life Histories and Habits of Some Grasshoppers of Economic Importance on the Great Plains. U. S. Dept. Agric. Tech. Bull., 774: 1–48.

Shotwell, R. L. 1942. Evaluation of Baits and Bait Ingredients Used in Grasshopper Control. U. S. Dept. Agric. Tech. Bull., 793: 1–51.

Swenk, M. H., and E. E. Wehr. 1923. Experiments with Poisoned Baits for Grasshoppers. Univ. Nebraska Coll. Agric. Exp. Sta. Bull., 183: 1–28.

Papers of the Michigan Academy of Science, Arts, and Letters
Vol. XLIII, 1958 (1957 Meeting)

NOTES ON NEARCTIC HELCOMYZIDAE AND DRYOMYZIDAE (DIPTERA ACALYPTRATAE)

GEORGE C. STEYSKAL
Grosse Ile, Michigan

Material which has recently come to hand provides interesting data in the little-studied family Helcomyzidae and additional data in the family Dryomyzidae, lately revised by me. (Steyskal, G. 1957. Pap. Mich. Acad. Sci., Arts, and Letters, 42: 55–68).

Family Helcomyzidae

Dryomyzidae Helcomyzinae Hendel, 1923, Konowia, 2: 213.
Helcomyzidae Malloch, 1933, Dipt. Patagonia and So. Chile, Pt. VI, Fasc. 4: 324; 1948, op. cit., Fasc. 6: 494.
Dryomyzidae pars Curran, 1934, Fam. Gen. No. Am. Dipt.: 382.
Dryomyzidae Helcomyzinae Séguy, 1934, Faune de France, 28: 86.
Helcomyziden Hennig, 1937, *in* Lindner, Die Fliegen d. pal. Reg., 5 (fasc. 52): 1.
Dryomyzidae Helcomyzinae Colyer and Hammond, 1951, Flies of the British Isles: 206.
Helcomyzidae Hennig, 1952, Die Larvenformen d. Dipt., 3: 245.
Dryomyzidae Helcomyzinae Brues, Melander, and Carpenter, 1954, Mus. Comp. Zool., Bull., 108: 367.

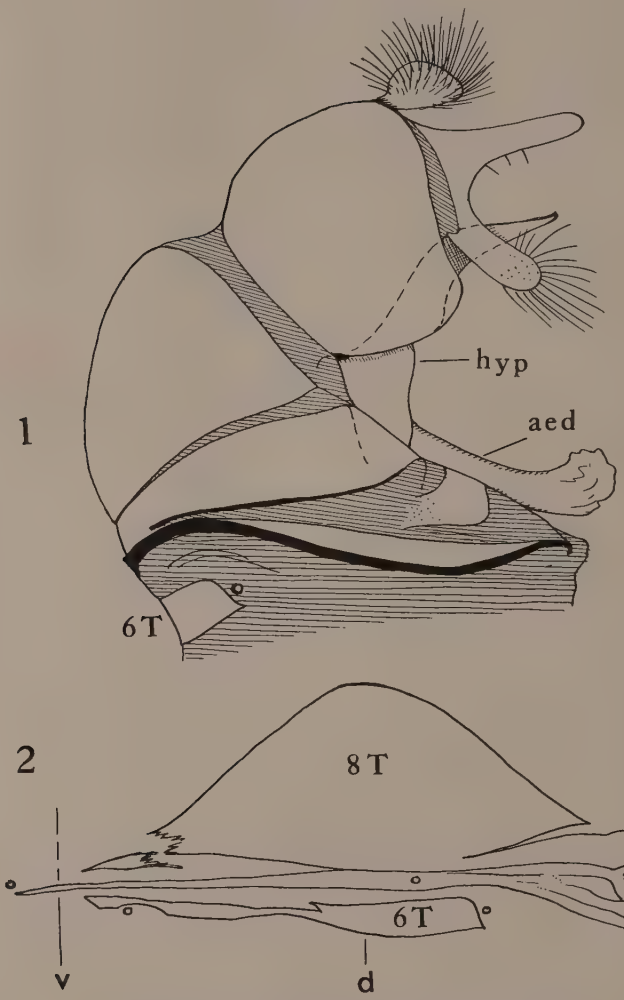
This group was long considered a part of the group centering about the genus *Dryomyza* and therefore included in the Dryomyzidae by those who gave that group family rank and in the Sciomyzidae by those who treated the group as a subfamily. As will be seen above, Malloch first raised the group to family rank, largely on the basis of a new character, that of the fusion between the prosternum and the propleura. Hennig discussed the group at some length, considering it to be of coordinate rank with the Dryomyzidae, Coelopidae, and Neottiophilidae. I would also subscribe to this view.

Only two species in North America are referable to the Helcomyzidae. These are listed below, with regional references, synonymy, and, for the first time, descriptions and figures of the male terminalia.

Helcomyza mirabilis Melander

(Figs. 1–2)

Helcomyza mirabilis Melander, 1920, Entom. Soc. Am., Ann., 13: 309; Cole and Lovett, 1921, California Acad. Sci., Proc., (4) 11 (15): 321.



Helcomyza mirabilis Mel., male, Boiler Bay, Oregon.

Fig. 1. Complete postabdomen, sinistral profile (hairs and bristles omitted, except on surstylus and cercus).

Fig. 2. Diagram of protandrium, drawn as if split ventrally and laid flat. *aed*—aedeagus; *d*—mid-dorsal line; *hyp* –hypandrium; *v*—mid-ventral line; *6T, 8T*—6th and 8th tergites.

Macromelanderia mirabilis (Melander) Curran, 1934, Fam. Gen. No. Am. Dipt.: 382; Hendel, 1935, Konowia, 14: 57.

The species was described from Ilwaco, Washington, and recorded by Cole and Lovett from Tillamook, Oregon, both localities on the Pacific Coast about 50 miles apart. I possess a pair from Boiler Bay, Oregon, about 45 miles south of Tillamook, received years ago through the courtesy of their collector, J. Wilcox. These specimens show all the characters ascribed to the genus *Helcomyza* by both Hendel and Malloch; accordingly, the genus *Macromelanderia* seems superfluous. Hendel asked "Wodurch unterscheidet sich *Macromelanderia* nov. gen. von. *Helcomyza*?"

The male terminalia of one of the Boiler Bay specimens is shown in Figs. 1 and 2. The protandrium, as diagramed in Fig. 2, has the sixth tergite well preserved and completely free, with both spiracles easily distinguishable; tergite 7 fused dorsally with tergite 8, but with both spiracles present, the dextral one dorsal in position and within the sclerite, the sinistral one slightly outside the sclerotic area in membrane. The epandrium (Fig. 1) has its anteroventral margins extended into a pair of long prongs turned inward and ventrad; both anterior and posterior surstyli fused into a common base, the anterior with many hairs on the mesal face. The hypandrium is rather simple with a median canal in which the aedeagus lies. The aedeagus is simple and tubiform, with a somewhat expanded, asymmetrical, soft glans.

Oedoparea buccata (Fallén)

(Figs. 3–7)

Heteromyza buccata Fallén, 1820, Heteromyzides Sveciae: 2; Walker, 1849, List. Dipt. Brit. Mus., 4: 1088.

Oedoparea buccata (Fallén) Loew, 1859, Zeits. Entom. Breslau, 13: 10.

Dryomyza hannai Cole, 1921, California Acad. Sci., Proc., (4) 11: 174.

Pseudosciomyza hannai (Cole) Malloch, 1923, No. Am. Fauna, 46: 215; 1933, Dipt. Patagonia and So. Chile, pt. 6, fasc. 4: 326.

Heterocheila nudiseta Curran, 1933, Am. Mus. Novitates, No. 673: 8.

This species was described from the Palaearctic Region and first noted from North America by Walker, who recorded it from Nova Scotia. Malloch in 1933 stated that "*Oedoparea* is represented (in North America) by *Pseudosciomyza hannai* Cole, a species very similar to *O. buccata*, Meigen (*sic*), but considerably darker in color." Cole based his description upon female material from St. Paul Island,

Alaska, and Malloch described the male from the same locality. I have examined material from St. Paul Island which could scarcely be called darker than *O. buccata* is described and which otherwise fits well. I am therefore, in the lack of authentic European material, tentatively considering *Dryomyza hannai* Cole to be the same as *Oedoparea buccata* (Fallén), and there seems also no reason for considering *Heterocheila nudiseta* Curran to be other than that species. The Canadian National Collection contains specimens of this species from Cold Bay, Alaska, 163° W., on tundra, 13 and 18 August, 1952, collected by W. R. M. Mason. A male from the Cold Bay collection has served for the preparation of Figs. 3–7 and the following description.

Protandrium (Figs. 3 and 5) with tergite 6 practically symmetrical, free and with both spiracles in membrane; sternite 6 free, but largely displaced to dextral side; tergite 7 and sternite 7 fused to each other and to tergite 8; both spiracles 7 in membrane. Epandrium without processes, but with posterior margin at each side of cerci deeply reflexed; surstyli placed well posterad, each consisting of one long slender arm and a short base slightly extended anterad (possibly fused anterior and posterior surstyli). Hypandrium (Figs. 3 and 6) with a group of hairs and a single bristle on each side. Aedeagus basally with broad, thin hood, anteriorly with blunt spine, and apically with complex, asymmetrical glans bearing several curved processes.

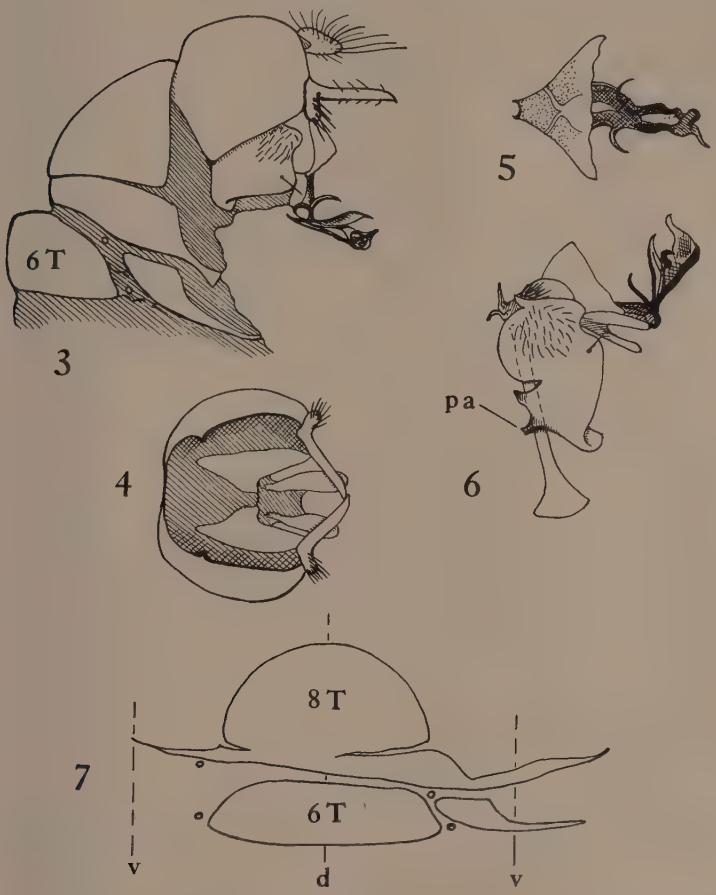
As will be seen below, another North American species, *Oedoparea glauca* Coquillett, has been found to be a Dryomyzid.

Family Dryomyzidae

In my revision, mentioned above, lack of satisfactory material prevented description and comparative study of the protandrium (abdominal somites 6–8). Such material has since come to hand. That in the Canadian National Collection has been the largest source of data, and thanks are especially due to Guy E. Shewell for making it available to me.

Dryomyza anilis Fallén

Additional records of importance were garnered from the Canadian material: *Alaska* (Anchorage; Cold Bay, 163° W., on tundra; Curry; King Salmon; Naknek River; Naknek, on tundra); *British Columbia* (Cultus Lake); *Ontario* (Marmora; Mer Bleue; Midland; Ogoki;



Oedoparea buccata (Flln.), male, Cold Bay, Alaska.

Fig. 3. Complete postabdomen, sinistral profile (hairs and bristles omitted from protandrium and epandrium).

Fig. 4. Ventral view of epandrium with inner copulatory apparatus removed.

Fig. 5. Posterior view of aedeagus.

Fig. 6. Inner copulatory apparatus. *pa*—point of attachment of hypandrium to epandrium.

Fig. 7. Diagram of protandrium, drawn as if split ventrally and laid flat. *d*—mid-dorsal line; *v*—mid-ventral line; *6T*, *8T*—6th and 8th tergites.

Ottawa); *Quebec* (Aylmer; Indian House Lake, approx. 56° N., 70° W.; Lac Mondor, Ste. Flore).

A diagram of the protandrium of this species was published in another recent paper. (Steyskal, G. 1957. Ent. Soc. Am., Ann., 50: 66–73).

Dryomyza bergi Steyskal

(Fig. 11)

Two additional specimens of this species were in the Canadian Collection, a male from Naknek, Alaska, on tundra, 8 August 1952, and a female from Naknek River, King Salmon, Alaska, 23 August 1952, both collected by W. R. M. Mason. Dissection of the male has enabled me to draw the diagram of the protandrium. Contrary to my statement in the original description, the aedeagus shows some fine pile posteriorly.

Dryomyza flaveola (Fabr.)

The Canadian National Collection has specimens from the following localities: *Alaska* (Naknek River, King Salmon; Naknek, on tundra; Paxson Lodge, Gulkana; Shaw Creek, mile 289, Richardson Highway); *British Columbia* (Salmon Arm); *Manitoba* (Wawanesa); *Ontario* (Marmora; Maynooth; Ottawa); *Quebec* (Indian House Lake, approx. 56° N., 70° W.; Messines; Mt. Orford); *Novia Scotia* (Kentville).

A diagram of the protandrium of this species also has appeared in my previously mentioned paper.

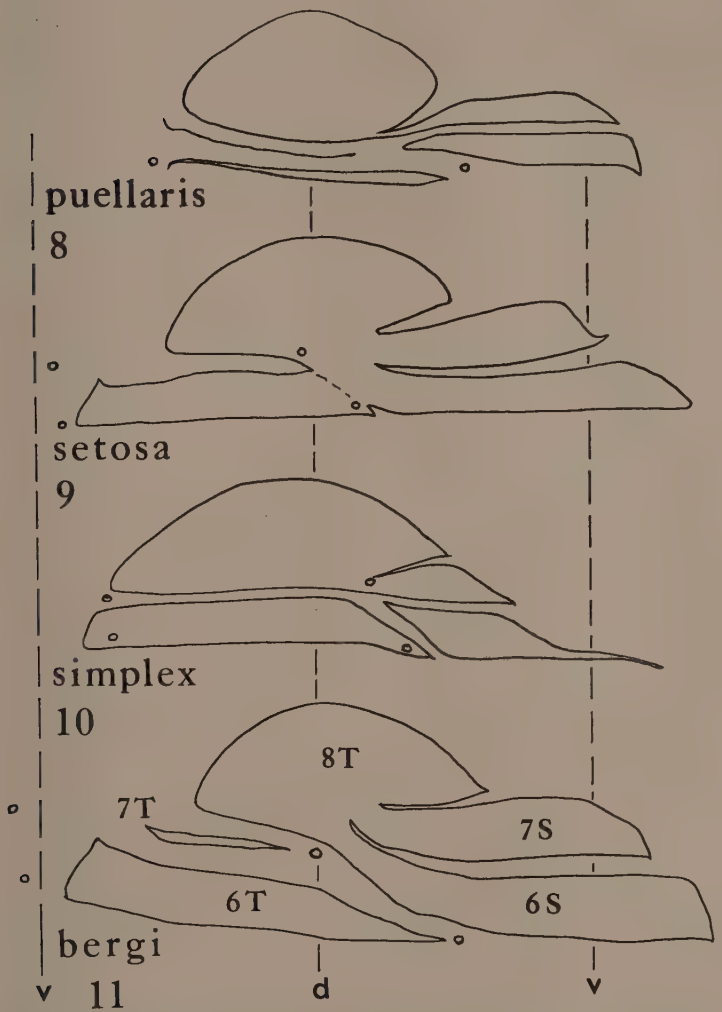
Dryomyza melanderi Steyskal

A single male specimen in the Canadian Collection from Agassiz, British Columbia, 16 June 1927 (H. H. Ross), shows that the protandrium and other features of the terminalia are very like those of *Dryomyza flaveola*, except that, as previously mentioned, the surstyli are longer.

Dryomyza setosa (Bigot)

(Fig. 9)

A male from Indian House Lake, Quebec, shows a protandrium as figured. The Canadian Collection contains specimens from *Alaska*



FIGS. 8–11. Diagrams of protandria of *Dryomyza* species, drawn as if split ventrally and laid flat. *d*—mid-dorsal line; *v*—mid-ventral line; *6S*, *7S*—6th and 7th sternites; *6T*, *7T*, *8T*—6th, 7th, and 8th tergites.

(Big Delta; Lake Boleo; mile 250, Richardson Highway); *Yukon Territory* (Rampart House); *Quebec* (Indian House Lake, approx. 56° N; 70° W.).

Dryomyza simplex Loew

(Fig. 10)

The Canadian Collection has a specimen from Midland, Ontario. A male from Dryden, New York, in my collection, served for the figure of the protandrium.

The protandrial diagrams listed above, together with the diagram of *Dryomyza puellaris* Steyskal, paratype (Fig. 8) and one of *D. formosa* (Wied.) in my cited paper, permit the following summary of the segmentation and spiraculation of the protandrium in the genus *Dryomyza*.

The following species have tergite 6 well developed, free from fusion with other tergites and accompanied by a distinct pair of spiracles: *Dryomyza anilis*, *D. bergi*, *D. formosa*, *D. puellaris*, and *D. simplex*. Of these, the spiracles are in the membrane in *D. anilis*, *D. puellaris*, and *D. bergi*; they are within the sclerite in *D. formosa* and *D. simplex*.

Tergite 6 is fused with tergite 8 dorsomedially in *D. flaveola* and *D. melanderi*. In *D. setosa* tergite 6 is fused with sternite 6. In all of these species, the dextral 6th spiracle is in membrane, the sinistral one in sclerotic tissue.

Tergite 7 is free only in *D. bergi*, although *D. puellaris* has a very slender band of sclerotic tissue that may be interpreted as tergite 7.

It is difficult to correlate the above characters with any of the other characters available to distinguish the species. However, *D. bergi* would seem to be the least specialized in protandrial segmentation and in possessing a surstylus unfused with epandrium and relatively simple aedeagus. *Dryomyza simplex* and *D. formosa* show relationship to each other in some respects, while in other ways they are as similar to other species. *Dryomyza flaveola* and *D. melanderi* are closely related and at the same time probably the most highly specialized. *Dryomyza anilis* is also highly specialized, but in other ways. It will be necessary to await knowledge of additional characters, including those of the immature stages, before a reasonable guess as to the phylogeny of the species of the genus is possible.

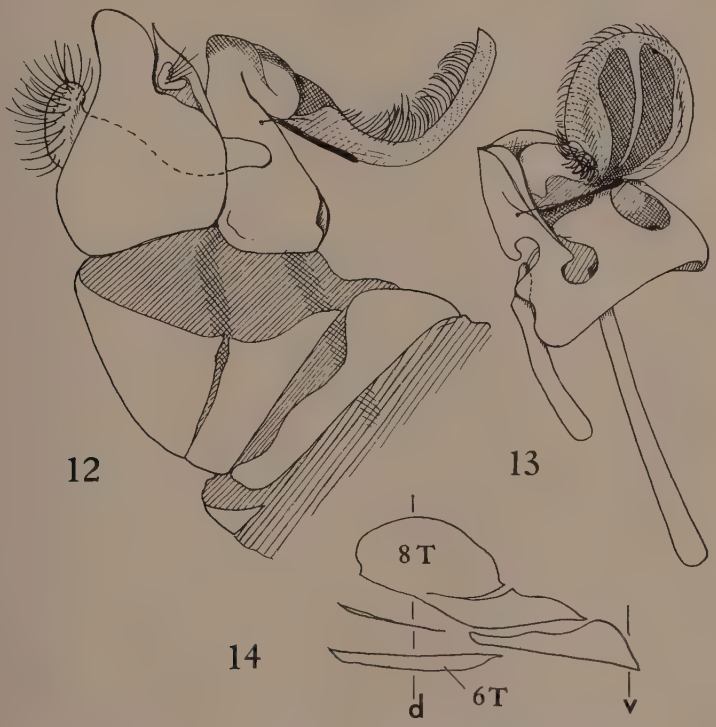
Oedoparena glauca (Coquillett)

(Figs. 12–14)

Oedoparea glauca Coquillett, 1900, Washington Acad. Sci., Proc., 2: 458; Hine, 1904, Canadian Entom., 36: 92; Cresson, 1920, Am. Entom. Soc., Trans., 46: 31.

Heterocheila glauca (Coq.) Aldrich, 1905, Smithsonian Misc. Coll., 46 (no. 144, Cat. No. Am. Dipt.): 578.

Heteromyza glauca (Coq.) Melander, 1920, Entom. Soc. Am., Ann., 13: 309; Saunders, 1928, Entom. Soc. Am., Ann., 21: 522.



Oedoparena glauca (Coq.), male lectotype, Metlakahtla, Alaska.

Fig. 12. Complete postabdomen, sinistral profile (hairs and bristles omitted from protandrium and epandrium).

Fig. 13. Anterolateral view of inner copulatory apparatus.

Fig. 14. Diagram of protandrium, drawn as if split ventrally and laid flat. *d*—mid-dorsal line; *v*—mid-ventral line; *6T*, *8T*—6th and 8th tergites.

Oedoparena glauca (Coq.) Curran, 1934, Fam. Gen. No. Am. Dipt.: 382.

Coquillett described this species from Metlakahtla and Farragut Bay, Alaska; Hine recorded it from Port Renfrew and Vancouver, British Columbia; Saunders recorded it also from Vancouver; and Melander cited its occurrence in Washington State.

I have examined the following material from the United States National Museum through the kindness of Curtis W. Sabrosky: one male, Metlakahtla, Alaska, 6–4–99; one male, Farragut Bay, Alaska, 6–5–99; two males, Smith Bay, California, VII-7 and 8, 1930 (J. M. Aldrich). The first two specimens are part of Coquillett's series of cotypes; I hereby designate the one from Metlakahtla as lectotype. The terminalia of the Metlakahtla specimen and the general characters of all four specimens show that they are very different from *Oedoparea buccata* and that they should be referred to the family Dryomyzidae in a genus distinct from *Dryomyza*.

Curran's name *Oedoparena*, based upon the presence of six scutellar bristles in *glauca* rather than four, is available. Additional characters are given in the key below.

Summary

Acalyptrate Diptera with the following characters form an apparently closely related group:

Wings with unbroken costa; subcosta complete and ending in costa.

Vibrissae lacking; prelabrum strongly developed, extending forward beyond medifacies.

Legs not greatly lengthened; at least some of tibiae with distinct dorsal preapical bristles.

Scutellum not greatly enlarged.

Metathoracic spiracle without bristles.

Postocellar bristles parallel or divergent.

The exclusively neotropical family Rhopalomeridae may be distinguished in this section by their protruding eyes, concave vertex, enlarged and heavily spined hind femora, and strongly spined hind tibiae. The remainder may be distinguished as follows.

KEY TO THE GENERA AND SPECIES OF NEARCTIC HELCOMYZIDAE AND DRYOMYZIDAE

Prosternum triangular, extending laterally to join the propleura; wing vein *m–cu* suppressed (vein closing second basal cell interstitial or almost so with vein closing

anal cell); third antennal segment no longer than high; cheeks with hairs from oral margin almost to eye; face narrowed below; antennae well separated at bases; wing sometimes with costal spines; male with fore and hind basitarsi simple *Helcomyzidae*

Middle tibiae with two rows of bristles posteriorly; costa with a few short spines; scutellum with dorsal setae; prosternum hairy; metasternum well developed, hairy; stigmatal bristle present; vein closing second basal cell and one closing anal cell forming a practically straight line *Helcomyza mirabilis* Melander

Middle tibiae with dorsal preapical bristle only; costa without spines; scutellum bare above; prosternum and metasternum bare; stigmatal bristle absent; veins closing second basal and anal cells both directed apicad to point where they meet ..... *Oedoparea buccata* (Fallén)

Prosternum narrow, strap-shaped or oval, well separated by membrane from propleura; vein *m–cu* distinct (vein closing second basal cell somewhat apicad of vein closing anal cell; third antennal segment longer than wide (except in *Oedoparena*); cheeks with extensive bare space between oral margin and eye (space reduced in *Oedoparena*); face widest below (only in *Dryomyza simplex* slightly narrower below); antennae only narrowly separated at bases; wings without costal spines; male fore and hind basitarsi usually with apical processes ..... *Dryomyzidae*

Middle of propleura and most of mesopleura furnished with soft hairs; pteropleura anteriorly with a few hairs; third antennal segmental circular in profile; middle tibiae with dorsal preapical bristle only; fore basitarsi of male with fingernail-like process ventrally; scutellum with six marginal bristles, apex pointed; dorsocentral bristles 4 or 5 +1 or 2; notopleurals 1; anterior notopleural and humeral usually indistinguishable among long hairs; prescutellars lacking; hypopleura bare; ocellars strong ..... *Oedoparena glauca* (Coquillett)

Middle of propleura, mesopleura, and pteropleura bare; third antennal segment longer than wide; middle tibiae usually with posterior row of bristles; fore and hind basitarsi of male with or without processes; scutellum with four marginal bristles, apex blunt; dorsocentrals 2, posterior; notopleurals 2; humeral 1; prescutellars present or lacking .... *Dryomyza* Fallén; see my revision for key to species.

BOTANY AND FORESTRY

Papers of the Michigan Academy of Science, Arts, and Letters
Vol. XLIII, 1958 (1957 Meeting)

STUDIES IN THE GENUS *FOMES*. I. SOME SYNONYMS

JOSIAH L. LOWE
State University of New York College of Forestry, Syracuse, New York

Many species of *Fomes* are distributed throughout the tropical areas of the world. This widespread occurrence may be due in part to a relatively uniform climate, persisting for ages, to similar substrata in the humid hardwood forests of the tropics, and to strong trade winds that carry spores long distances. The actual distribution of some other tropical species may be obscured by the use of different names for the same fungus in widely separated areas, or by renaming when the original description was inadequate or inaccurate. Uncovering such synonyms clarifies the taxonomic and distribution problems in the genus, and is in itself fertile and interesting research. My studies in the genus *Fomes* have demonstrated four examples of unsuspected synonymy. Two of these connect Old World and New World species, and two connect species described from southeast Asia.

The studies reported here were made in the herbaria of the National Fungus Collections of the U. S. Department of Agriculture at Beltsville, Maryland. I am most grateful to Mr. John Stevenson for the privilege of studying the specimens under his care and for financial support as a collaborator while making these studies.

Fomes floccosus (Bres.) Lloyd
(*Polyporus farinosus* Lloyd)

This species was described from Africa. Its distinguishing characteristics are the eventually rather large sporophore, up to 20 cm. broad and 9 cm. thick, with a brownish to slate-colored upper surface, the punky cream-colored context, about 3 pores per mm., and hyaline narrowly elliptical spores "12–14 × 5–7 μ" (Bresadola), or "16–18 × 7–8 μ" (Petch, herbarium notes). The fungus is the same as a specimen collected by Rick and described by Lloyd (1915, p. 337) as *Polyporus farinosus*. The same material was the basis of a new species earlier proposed by Rick (1907) and published in a confused manner,

as *Polyporus cartilaginosus* on p. 85 and illustrated under the name *P. farinosus*, Tab. 4, Fig. 4. Rick's collections agree with Ceylon material identified by Lloyd except that the pores are somewhat larger, about 2 per mm. In addition to its type locality in central Africa, Lloyd (1920, p. 1010) reported that *F. floccosus* is found in India, Ceylon, and Australia. The synonymy reported here extends its range to Brazil.

In his notes on the Ceylon collection Lloyd (1920, p. 1010) restored the species to its original genus *Trametes*, which appears to be a better disposition than *Fomes*.

Fomes melanodermus (Pat.) Sacc. & Syd.

(*Fomes oroniger* Lloyd)

This species was described from Java and its diagnostic characteristics are the glabrous crust, conspicuous setal hyphae in the trama, and yellowish-brown spores 3–4 × 2.5–3.5 μ. I propose *Fomes oroniger* as a new synonym. Lloyd (1924, p. 1330) described it from Singapore, basing the specific name on the black pore mouths. Lloyd's type specimen is an abnormal one, with the pore surface covered with a black crust. Lloyd states further that the type had no setae, and lacked spores, which he surmised were hyaline. Careful study, however, demonstrates that in well-developed tubes there were abundant setal hyphae, setae, and brown spores that agree with these details in type material of *F. melanodermus*. I consider *F. oroniger* a teratological form of that species. Lloyd (1922–24, p. 1164, 1299) further reports *F. melanodermus* from Ceylon, the Philippines, and Brazil. The synonymy proposed would establish it also in Malaya.

Fomes ochroleucus (Berk.) Lloyd

(*Polyporus turbinatus* Pat.)

This species was described from Australia as a *Polyporus*. Much later it was referred to *Fomes* by Lloyd (1917, p. 714), who received typical perennial specimens from the same country. The diagnostic characteristics of the species are the pale context and the large truncate spores 13–17 × 7–10 μ. These are the distinguishing features of *Polyporus turbinatus* Pat., which I consider a synonym. Cunningham (1948, p. 5) reports *F. ochroleucus* from Tasmania, Australia, New

Zealand, Ceylon, Japan, and Portugal. The present synonymy would extend the distribution to the New World, to Venezuela, where *P. turbinatus* is known only from the type material. Records of *F. turbinatus* (Pat.) Murr. from the West Indies by Murrill (1915, p. 75) should be referred to *F. ohiensis* (Berk.) Murr., a very similar species which differs principally in having spores 10–13 × 5–8 μ.

Fomes sanfordii Lloyd

(*Fomes inflexibilis* var. *javanicus* Bres.)

This species was described from Ceylon in 1915. Its outstanding characteristic, which suggested the specific name, is the intense color of the context, which is exactly Sanford's Brown of Ridgway's *Color Standards*. The only other *Fomes* with similarly colored context was described from Java by Bresadola in 1912 as *F. inflexibilis* var. *javanicus*. Isotype material of the variety appears wholly unrelated to the type material of *F. inflexibilis*; it is much more similar to *F. sanfordii* and differs only in the relative abundance of setae, which are rare in var. *javanicus*, and usually frequent in *F. sanfordii*. I consider the synonymy certain. The valid name is *F. sanfordii*, as the species epithet takes precedence over the varietal name. The fungus is known with certainty from Ceylon and Java; an additional collection from Japan, determined as *F. sanfordii* by Lloyd, may be a different species.

LITERATURE CITED

Cunningham, G. H. 1948. New Zealand Polyporaceae. 5. The Genus Fomitopsis. N. Z. Plant Diseases Div. Bul., 76:1–8, plates 1–3.

Murrill, W. A. 1915. Tropical Polypores. i–iv; 1–113. New York, N. Y. Privately printed.

Lloyd, C. G. 1912–1925. Mycological Writings of C. G. Lloyd. Cincinnati, Ohio. Vols. 4–7.

Rick, J. 1907. Contributio ad monographiam Agaricacearum et Polyporacearum Brasiliensium. Broteria, 6:65–92. Tab. 1–9.

Papers of the Michigan Academy of Science, Arts, and Letters
Vol. XLIII, 1958 (1957 Meeting)

CRUISING POLE TIMBER BY BITTERLICH'S ANGLE-COUNT METHOD

JOHN CAROW
University of Michigan

Since Grosenbaugh introduced Bitterlich's method of direct basal area determination to American foresters in 1952, the use of this fascinating new technique for density determination in cruising has increased rapidly despite conflicting reports with regard to its accuracy and a general lack of good mensurational tables to go with it. Research has lagged conspicuously behind application, with the result that the theory has been imperfectly understood and the method often improperly applied. Even the instruments have been expedients. Good instruments are not yet commercially available at reasonable prices despite some good work by Bruce (1955) and others, and the availability of prior European experience.

The purpose of this paper is to examine some of the problems that have come to my attention and to give a preliminary report on an investigation I have been making into one aspect of it.

Bitterlich's angle-count method provides a basal area estimate by the simple process of counting around one or more points in the forest all the trees whose diameters appear to intercept the sides of a small horizontal angle projected from the observer's eye by an optical sighting device. The tree count multiplied by a constant that is related to the size of the angle gives the estimate of basal area per acre. As with any sampling scheme, a number of point counts are needed to get a reliable estimate of the average density over a whole stand. The theory of the Bitterlich method has been explained in a number of articles (Afanasiev, 1957; Grosenbaugh, 1952).

While the Bitterlich method gives basal area directly, most interest centers around its use in cruising. Volume estimates have been made in two ways. Tables of volume per square feet of basal area can be adapted from existing volume tables or made directly from tree measurements. These tables generally show that tree to tree variation is related principally to height and only to a minor degree to dbh since dbh enters into both parts of the volume basal area ratio

and thus cancels out. In practice, then, trees counted in the basal area estimate need only be tallied by height classes, and this can be done quickly by one man from his counting point at a fraction of the plot-taking time required with fixed radius plots.

The second volume-estimating scheme is to utilize stand volume tables which give volume per acre based on basal area per acre and height. The angle count gives basal area, and a few height measurements complete the work necessary to read the estimate from the table. Again, the average of a number of points improves the stand estimate. The stand volume table method has been little used in America, but it is widely employed in northern European countries.

Tests with angle-count cruising have shown that volume estimates are generally more erratic than basal area estimates. This is to be expected, since volume determination introduces an extra step in the estimating process and thus is subject to more variation. Investigations in the use of Bitterlich's technique can generally be confined to basal area with the sure knowledge that volume will behave similarly with some additional error.

Most of the angle gauges used in this country measure a 104.18-minute angle because it has the very convenient basal area factor of 10, and because it works well in sawtimber-sized stands. Trees, 20 inches in dbh, for example, are tallied if within 55 feet of the counting point. This corresponds then to the $\frac{1}{5}$-acre circular plot which has been much used in such timber. With pole timber of 8-inch dbh, however, the 10-factor gauge counts only trees within 22 feet from the point, corresponding to a 0.035 acre plot. I think anyone with experience in pulpwood cruising will tell you that this is too small a plot size. Small plots tend to give erratic results because the clustering of trees gives individual plot estimates that are too high or too low; and, with high variance, more samples must be taken to attain the error standards common to cruises using larger plots.

A few years ago the Forest Service made a study of angle-count cruising in the Upper Peninsula to test its feasibility for administrative use in the National Forests. This was a private study, but I was privileged to review the report. Tests were made in several pole and small sawtimber stands using both the 10-factor gauge and conventional $\frac{1}{5}$-acre fixed radius plots. As might have been expected the angle-count estimates had greater variance, and the report seriously questioned the advisability of using the technique. It suggested that

perhaps 1/10-acre fixed radius plots would give results of comparable accuracy and speed. No attempt was made in that study to try other angles, which would take larger samples and thus reduce variance.

An Investigation into Angle Sizes for Use in Pole Stands

From some early investigations done by Stage and other students working with me (Carow, 1952), it has always seemed that the size of the angle gauge might well be altered to fit the timber just as we sometimes alter the size of fixed radius plots under changes in timber conditions. In the summer of 1954 I designed a study to test three different-sized angle gauges in pulpwood timber for the purpose of determining variances involved with each angle and the relative plot-taking time. The field work was done by two student assistants at the close of the summer session in the vicinity of Camp Filibert Roth, with the support of a small grant from Rackham research funds. A total of 35 points was sampled in timber ranging from 6 to 14 inches in diameter and of varying degrees of density in pine, spruce, and aspen types. A Spiegel-Relaskop designed by Bitterlich was used for the tests and three angle counts and a conventional 1/5-acre circular plot were taken about each of the sample points. The angles used and their associated factors are given in Table I.

The Spiegel-Relaskop is an instrument somewhat similar in appearance and action to the Forest Service hypsometer. When it is held to the eye, the sighted tree and a series of angle gauges are optically focused for easy comparison. The gauges fastened to a pendulum in the instrument are automatically adjusted to the ground slope, so that tree counts are comparable to those that would be obtained on

TABLE I

Critical Angles Used in Tests

Critical Angle	Basal Area Factor	Ratio: dbh to counting radius	Equivalent plot size for 8″ trees	
			radius	acres
minutes				
49.0	2.178	1:70.7	47′	0.16
69.0	4.356	1:50	33′	0.08
97.4	8.712	1:35.3	24′	0.04

level ground. Our instrument was graduated in metric units, which accounts for the decimal basal area factors. I selected the factors of Table I as those nearest to the 2, 5, and 10 which would be simplest to use in our American unit system.

At each of our sampling points trees were first tallied using the largest angle and obtaining the smallest count. Then successive counts were made with the middle-sized and with the smallest angle. A tree counted by one gauge would also be counted by those with smaller angles. Finally the 1/5-acre plot was taken with each tree being taped for dbh. Heights are tallied for each tree on each sample in 8-foot bolt lengths to a merchantable top. Tallied trees were marked so that the same height estimate was made on successive cruises. No attempt was made to time the work on the 35 plots used for the precision tests. Later, time data was taken at similar points in similar timber using each of the gauges and the 1/5-acre plots.

Results

Table II gives the coefficients of variation and the standard errors relative to the means that were observed for the whole 35 point sample. The coefficients are in the order one would expect, with the 1/5-acre plot having the least variation and the others increasing as effective plot size decreased. An examination of the errors within some arbitrary density groups in the sample reveals that the standard error in per cent of the mean was least in stands of high basal area and greatest in the sparse densities. When basal areas by angle count were compared with those of the plots correlation coefficients of 0.93 were observed with the two smaller angles and 0.81 with the 97.4-minute angle. This, too, verifies the expectation that the small count samples are most erratic. All the correlations were significant.

TABLE II

Coefficients of Variation and Standard Error of the Mean

Sampling Unit	Coefficient of Variation	Standard Error of Mean
1/5-acre plot	±35.0 per cent	±5.9 per cent
49.0′ angle count	±38.7	±6.5
69.0′ angle count	±38.7	±6.7
97.4′ angle count	±42.9	±7.2

TABLE III

COMPARATIVE PLOT-TAKING EFFICIENCY

Sampling Unit	Average Time per Plot	Number of Points to Equal Accuracy of 1/5A.	Time for Same Accuracy
1/5-acre plot	16.2 minutes	1.0	16.2 min.
49.0′ angle-count	9.7	1.21	11.7
69.0′ angle-count	5.8	1.23	7.1
97.4′ angle-count	3.4	1.5	5.1

Large gauge angles with their small counts allow quicker plot work than the smaller angles that include more trees. Efficiency in plot-taking can be compared by computing the time needed to attain the same accuracy by each of several alternate procedures. The results given in Table III summarize the findings in this regard. The plot-taking times are averages of three of us working individually in a variety of densities and taking usual cruise data in addition to the sample tree counts.

According to our investigation the 97.4-minute angle plot had a higher standard error than those with larger tree counts and would require half again as many point counts for an accuracy comparable to the use of the 1/5-acre sampling unit. The plot-taking, however, was enough faster to offset this disadvantage and require only five minutes for data collection of a value equivalent to the 16 minutes needed with a single fixed radius plot. The two smaller gauge angles tested were about equal in terms of standard error, but the smaller angle took too much tallying time.

The 69-minute angle had good accuracy and could be done with sufficient speed to exceed the efficiency of the fixed radius plot, but in this test its efficiency was not superior to the 97.4-minute angle as I had expected.

My test did not consider travel time between points. If the criterion had been acres cruised to the same error standard in an 8-hour day, then travel time could be important. By placing the extra samples needed with the 97.4-minute angle on the same cruise lines no additional travel time would be needed, but if another cruise line were required in a tract, then the smaller, more variable sampling

unit would cost more for travel and larger plots would become advantageous.

There are, of course, many unanswered questions regarding angle-count cruising. More conclusive work is needed on the problem presented and it should be made more complete by investigating travel time and by looking into the possibilities and problems of cluster sampling. A better understanding is also needed of bias observed in many tests. We have found that in using instruments such as the Relaskop there is definite personal bias in judging line trees, but we have not studied it closely. There are also opportunities in instrument design and in the preparation of mensurational tables. Foresters are using the angle-count technique, and research must be stepped up to solve some of the problems and to provide useful data.

LITERATURE CITED

Afanasiev, Michael. 1957. The Bitterlich Method of Cruising—How Does It Work? Journ. Forestry, 55:216–217.

Bruce, David. 1955. A New Way to Look at Trees. Journ. Forestry, 53:163–166.

Carow, John. 1952. Bitterlich's Method of Direct Basal Area Estimation. Pap. Mich. Acad. Sci., Arts, and Letters, 28:125–132.

Grosenbaugh, L. R. 1952. Plotless Timber Estimates—New, Fast, Easy. Journ. Forestry, 53:32–37.